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Vol. 78, No. 2 April 1980

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Fishery Bulletin

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A SURVEY OF CIGUATERA AT ENEWETAK AND BIKINI, MARSHALL ISLANDS, WITH NOTES ON THE SYSTEMATICS AND FOOD HABITS OF CIGUATOXIC FISHES[1]

JOHN E. RANDALL[2]

ABSTRACT

A total of 551 specimens of 48 species of potentially ciguatoxic fishes from Enewetak and 256 specimens of 23 species from Bikini, Marshall Islands, were tested for ciguatoxin by feeding liver or liver and viscera from these fishes to mongooses at 10% body weight (except for sharks, when only muscle tissue was used.) The fishes are representatives of the following families: Orectolobidae, Carcharhinidae, Dasyatidae, Muraenidae, Holocentridae, Sphyraenidae, Mugilidae, Serranidae, Lutjanidae, Lethrinidae, Carangidae, Scombridae, Labridae, Scaridae, Acanthuridae, and Balistidae. The species selected were all ones for which toxicity can be expected, including the worst offenders from reports of ciguatera throughout Oceania; only moderate to large-sized adults were tested. In all, 37.3% of the fishes from Enewetak and 19.7% from Bikini gave a positive reaction for ciguatoxin. Because liver and other viscera are more toxic than muscle, the percentage of positive reactions at the level which might cause illness in humans eating only the flesh of these fishes collectively would drop to 16.2 for Enewetak and 1.4 for Bikini. This level of toxicity is not regarded as high for Pacific islands, in general.

Because ciguatoxin is acquired through feeding, the food habits of these fishes were investigated. Most of the highly toxic species, including seven of the eight causing severe illness or death in the test animals (*Lycodontis javanicus*, *Cephalopholis argus*, *Epinephelus hoedtii*, *E. microdon*, *Plectropomus leopardus*, *Aprion virescens*, and *Lutjanus bohar*) are primarily piscivorous. Some such as *Lethrinus kallopterus* (which also produced a mongoose death) feed mainly on echinoids and mollusks. Among the larger herbivorous fishes that were tested, only one individual of *Kyphosus* and two of *Scarus* caused a weak reaction in the test animals.

In view of the importance of correct identification of the ciguatoxic fishes, diagnostic remarks and an illustration are provided for each of the species tested. Some alteration in scientific names was necessary for a few of the fishes.

The Marshall Islands are the easternmost islands of Micronesia and of the Trust Territory of the Pacific Islands. They consist of 34 low islands, most of which are atolls, and numerous reefs which occur between lat. 4°30′ and 15°N and long. 161° and 173° E. They lie in two parallel groups in a northeast-southwest direction, the easternmost being the Ratak ("Sunrise") Chain and the westernmost the Ralik ("Sunset") Chain.

Two types of fish poisoning are known from the Marshall Islands: tetraodontid (puffer) poisoning (Hiyama 1943; Yudkin 1944; Halstead 1967) and ciguatera. This paper is restricted to the latter toxemia. It results from the ingestion of a great variety of tropical reef and semipelagic fishes. Ciguatoxin is thermostable, hence unaffected by cooking or freezing of the fishes. It is not the result of decomposition but is present to a varying degree in the different tissues of fishes when entirely fresh. The severity of the illness and the symptomatology depend upon the concentration of the toxin and the amount of fish eaten; fatalities are rare. Symptoms appear about 1-10 h after a toxic fish is consumed; those most commonly given are: weakness or prostration; diarrhea; tingling or numbness of the lips, hands, and feet; confusion of the sensations heat and cold; nausea; joint and muscular pain; inability to coordinate voluntary muscular movements; difficulty in breathing; burning urination; and itching. Probably the most common diagnostic symptoms are unpleasant tingling sensations of the palms of the hands and soles of the feet on contact with cool materials and the feeling of heat when cold objects are touched or cold liquids taken into the mouth. Light cases may not exhibit these sensations, however.

The Marshall Islands have long been known to harbor ciguatoxic fishes. The earliest report from these islands seems to be that of Steinbach (1895) who wrote of fishes being toxic on the west side of

[1]Contribution of the Mid-Pacific Research Laboratory.

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the lagoon at Jaluit. Becke (1901) recorded poisonous fishes from Ralik (Ebon), the southernmost atoll in the Marshalls (reference from Halstead 1967). With the takeover of the Marshalls by Japan at the start of World War I (1914), the documentation of ciguatera at these islands shifted to the Japanese. Hishikari (1921), Matsuo (1934), and Hiyama (1943) published on poisonous fishes at Jaluit. Some fishes in the vicinity of Utirik Island, Utirik Atoll, have been reported as poisonous (Hydrographic Office, U.S. Navy 1945).

Historically, Jaluit was the principal atoll of the Marshalls. It was the center of government, had the greatest shipping activity, and the highest population (1,683 in 1933). As a result of military activity during World War II, Kwajalein (the largest atoll in the world) and Majuro became more important. Majuro is the District Administrative Center of the islands. By 1958 the population was 3,336 (compared with 783 in 1935), whereas the population at Jaluit had declined to 1,112 in 1958 (Robson 1959).

Concurrent with the buildup in population and commerce at Majuro and Kwajalein was the appearance of ciguatera (or at least the first records in the literature of its incidence). Halstead and Lively (1954) reported one death and five persons seriously ill from the consumption of a moray eel at Kwajalein. Bartsch et al. (1959, table 2) documented the marked increase in cases of fish poisoning at the hospital at Majuro; there were 22 in 1955 (all in the last half of the year), 100 in 1956, and 211 in 1957. Banner and Helfrich (1964) stated that the atolls in the Marshall Islands where poisonous fishes are most commonly found are Kwajalein, Mille, Ailinglaplap, Jaluit, and Majuro. They tested numerous fishes of many species from Enewetak (formerly spelled Eniwetok) collected in 1958, but none were found to be toxic. Balaz,[3] on the other hand, interviewed Chief Johannes, the last remaining traditional chief of the Enewetak people, at Majuro on 15 March 1974. Johannes stated that poisonous fishes were known at the atoll at the time of his departure in 1946 from the islands of the eastern side between the deep passage and the northern end. It should be pointed out, however, that a short-term field survey of ciguatera at an atoll, such as that carried out by Banner and Helfrich, is difficult to equate to the continuous human bioassay of a population of native people dependent on fishes as their principal source of protein. One should also emphasize that even in highly toxic sectors, the percentage of poisonous fishes that will cause ciguatera when eaten is small. Nevertheless, only a few cases in an area may be needed to prevent residents from fishing in that area.

The atolls of Enewetak and Bikini are located at the northern end of the Ratak Chain 165 mi apart between lat. 11° and 12° N. The native people of Bikini were moved from their island to Rongerik Atoll and later to Kili Island when a series of nuclear explosion tests were carried out by the United States beginning in 1946. The people of Enewetak were transferrred to Ujelang Atoll in 1947 for the same reason. When repatriation of these Micronesian people was contemplated, a question arose as to the current level of toxicity of the food fishes of Bikini and Enewetak.

Fluctuation in the toxicity of fishes in reef ecosystems has long been recognized (Banner and Helfrich 1964; Cooper 1964; Halstead 1967; and Helfrich and Banner 1968). Furthermore, Randall (1958) hypothesized that disruptions of the marine environment resulting in the creation of new surfaces (particularly the repetitive formation of new surfaces) in potentially ciguatoxic areas may be linked to outbreaks of the toxemia. This hypothesis has received support from Cooper (1964) who related toxic sectors in the Gilbert Islands to the locations of wrecks and anchorages, by Helfrich et al. (1968) who documented the first outbreak of ciguatera at Washington Island, Line Islands, following the wreck of the MS *Southbank* in late 1964, and by Bagnis (1969) who reported numerous cases of ciguatera at the previously nontoxic atoll of Hao in the Tuamotu Archipelago after the atoll was altered as a staging area for nuclear testing at Mururoa.

de Sylva (1963) misinterpreted this hypothesis. He stated that Randall found poisonous fishes in estuarine areas. On the contrary, Randall reported toxic fishes in the Society Islands from certain areas of slight or intermittent freshwater drainage which are ordinarily flushed with clear water from the open sea. During periods of heavy rain the freshwater runoff to a normally marine habitat may cause death of stenohaline sessile marine animals, thus forming a new surface for benthic growth.

After stating that the basic toxic organism must be benthic, Randall (1958) wrote, "Since obligately herbivorous fishes and detritus-feeding

[3]George H. Balaz, Research Associate, Hawaii Institute of Marine Biology, pers. commun. 1974.

fishes may be poisonous, the toxic organism would most likely be an alga, a fungus, a protozoan, or a bacterium." He added that if it were an alga it must be fine because certain potentially toxic surgeonfishes are unable to feed on coarse types. Of the algae, he wrote that blue-greens were the most probable source of ciguatoxin.

Yasumoto et al. (1977), however, have shown that the "likely culprit" of ciguatera is a dinoflagellate which lives attached to dead coral or benthic algae. Though identified initially as a new species of *Diplopsalis*, it was later shown (Taylor 1979) to be a new genus as well. Subsequently, Adachi and Fukuyo (1979) named it *Gambierdiscus toxicus*. Although a fat-soluble toxin, later identified as ciguatoxin, was isolated from wild dinoflagellates of this species, this organism produced "... only meager amounts of ciguatoxin, if any,..." under culture conditions (Yasumoto et al. 1979).

The author first visited Enewetak in 1967, then in use as the terminus of a missile range by the United States. The resident personnel had been informed of the hazard of ciguatera, and local reef fishes were not served in the mess. In spite of the warning, some cases of ciguatera still occur, especially with the crews on supply ships to the island who sometimes catch and eat fishes, particularly red snapper, *Lutjanus bohar*, from the vessels before they could be informed of the danger. The most recent case was reported by Roth.[4]

In 1968 six residents of the atoll ate a large reddish brown grouper with small blue spots (probably *Plectropomus leopardus*) that one of them had caught off the garbage pier at the southwest end of Enewetak Island. They had asked a cook in the mess hall to prepare the fish for a meal. The cook refused, explaining that the species was one which could make them sick. Disbelieving, the men took the fish to their quarters and cooked it themselves. They all contracted ciguatera and were hospitalized (Spillman).[5]

These cases of fish poisoning and the knowledge that the marine environments of both Enewetak and Bikini have indeed been disrupted underlined the need for a survey of ciguatera at the two atolls.

The survey was supported by the U.S. Energy Research and Development Administration (now Department of Energy). The field work at Enewetak was based at the Mid-Pacific Marine Laboratory, and the fishing at Bikini was carried out from the RV *Liktañur*.[6] The testing of fishes for ciguatoxin was done at the Hawaii Institute of Marine Biology, University of Hawaii, under the supervision of A. H. Banner.

Six fishing expeditions of 2 to 4 wk duration were dispatched from Hawaii to Enewetak within the period September 1974-May 1978. There were four fishing cruises to Bikini (fishing periods of 3-7 days at the atoll) from December 1974 to July 1976. In addition, 12 potentially toxic *L. bohar* were caught from the *Liktañur* at the atoll of Rongelap in November 1975.

Fishes were collected by spearing, hook and line, trolling lures, explosives, and the ichthyocide rotenone. The specimens were held in chests of crushed ice until they were returned either to the Mid-Pacific Marine Laboratory or the *Liktañur*. They were then measured and weighed, tagged with a metal tag, and a sample taken for testing which included the liver, other viscera, and muscle. A data sheet was filled out for each specimen; the upper half of each sheet was used for field data and the lower half to record the testing for toxicity. A chart of the atoll was printed on the back of each data sheet (separate sets of sheets were maintained for Enewetak and Bikini) so that the locality of capture could be recorded. At Enewetak the entire fish was frozen after the sample was taken for testing. Aboard the *Liktañur* only the samples were retained. The Enewetak specimens, which proved to be highly toxic (rated 4 or 5, see below), were transported frozen to the University of Hawaii for use in biochemical and pharmacological research on ciguatoxin; the remaining fishes were either discarded or used as bait or chum.

For the testing, the samples of fish were fed to mongooses (*Herpestes mungo*) in single meals at 10% body weight. The mongoose is a good animal for the bioassay of ciguatoxin (Banner et al. 1960) because it has a symptomology similar to humans suffering from ciguatera, it retains a meal of toxic fishes (in contrast to cats which are prone to regurgitate fish when it is very poisonous), and because of its availability in Hawaii (where it is regarded as a pest). The mongoose symptoms were

[4]Robert M. Roth, Capt. USAF, MC., Command Surgeon, Joint Task Group, Enewetak, described the illness (symptoms typical of ciguatera) of Francisco Romolor, age 28, a civilian deckhand on the cargo ship *Muskingum*, following ingestion of a red snapper caught in the lagoon (pers. commun. 2 June 1978).

[5]Louis C. Spillman, Jr., Chief Medical Officer, Enewetak, pers. commun. 1968.

[6]The RV *Liktañur* is a converted U.S. Navy LCM, 115 ft in length, operated then by the U.S. Energy Research and Development Administration as a research and supply vessel.

divided into five progressive categories from 1 (diarrhea, slight weakness, and flexion of the forelimbs) to 5 (death within 48 h). The lack of symptoms was recorded as 0. The tests which resulted in a reaction of 4 or 5 were repeated on other mongooses if sufficient material was available. Also any questionable or unexpected tests were repeated.

Two tests were run on most of the fishes, one based on the feeding of liver or liver and viscera to the mongooses and one on muscle tissue. The liver of a toxic fish invariably gave a stronger reaction than muscle. A reaction of 3 to liver feeding would generally elicit a reaction of 1 with flesh. Helfrich et al. (1968) found liver more than 50 times as toxic as the muscle tissue of *L. bohar*. The remaining viscera are also more toxic than somatic muscle. Since the liver alone was often insufficient in mass to provide a meal to a mongoose at 10% body weight, it was usually necessary to combine it with other viscera (generally alimentary tract tissue).

The level of toxicity reported herein is from the liver-viscera feeding, with the exception of sharks. Shark liver may cause a toxemia from the high level of vitamin A. Furthermore, it was noted that mongooses will either not eat shark liver or will not consume enough to equal 10% of their body weight. Thus the toxicity data on sharks are based on muscle tissue alone.

Once a mongoose exhibited symptoms of ciguatera, it was not used again for testing. If it showed no symptoms at all, it was used a second time, but only after a period of at least 1 wk had elapsed. No mongooses were fed potentially toxic fish more than three times even when no symptoms were elicited. The reason for this is the known tendency for ciguatoxin to accumulate in a test animal. Though a fish may cause no illness when eaten, it may still have some toxin at the subsymptomatic level. Eating several such fishes in succession might result in a positive test for the last one, even though there was insufficient toxin to produce illness in a mongoose consuming such a fish for the first time.

The results of our first sampling of potentially toxic fishes at Enewetak and Bikini did not indicate a high level of toxicity. Only the larger individuals of the usual offending species were poisonous. Most of these species are carnivores, in particular those feeding heavily on fishes (Randall 1958). Therefore, subsequent fishing was concentrated on the larger fishes of these species. Because of this selectivity, both for species and size, more fishing effort was spent per fish caught; however, this meant less effort expended later in useless testing.

Prior to the present study, information on the food habits of ciguatoxic fishes was insufficient for most species. When a trained marine biologist familiar with the Marshallese marine biota was present, an analysis was made of the stomach contents of the fishes that were caught. Since ciguatoxin is known to pass through food chains to the larger fishes, where it is concentrated, analyses of the stomach contents of these fishes are needed for an understanding of the feeding interrelationships.

Some previously unpublished stomach-content

TABLE 1.—Summary of mongoose feeding tests (liver-viscera, sharks excepted) of fishes collected at Enewetak (0 = nontoxic; 5 = death of test animal).

Species	Intensity of reaction					
	0	1	2	3	4	5
Nebrius ferrugineus	2					
Carcharhinus albimarginatus	4					
C. amblyrhynchos	11		1			
C. galapagensis	1					
C. limbatus			1			
Galeocerdo cuvier	2					
Triaenodon obesus	8					
Taeniura melanospilos	1					
Lycodontis javanicus			2	1	3	3
Adioryx spiniter	6					
Sphyraena barracuda	3	1	2	1		
Cephalophalis argus	2	3	3		1	
Epinephelus fuscoguttatus	2		4	1		
E. hoedtii	6	3	1		1	
E. maculatus	8	3				
E. microdon	8	3	8	13	5	2
E. socialis	2					
E. tauvina	4	1	1			
Plectropomus leopardus	12	6	8	4		1
P. melanoleucus			1			
P. truncatus			1			
Variola louti	13	4		2		
Aprion virescens	8	1		1	1	
Lutjanus bohar	56	22	11	5		1
L. fulvus	2					
L. gibbus	21	5	2	3		
L. monostigmus	1	1	1			
Macolor niger	23	2				
Lethrinus amboinensis	24					
L. kallopterus	14	2	2			1
L. miniatus	6			3		
L. xanthochilus	2					
Monotaxis grandoculis	4	1				
Kyphosus cinerascens	1	1				
Caranx ignobilis	3	2				
C. lugubris	11	2	1	1		
C. melampygus	24	4	1	1		
C. sexfasciatus	2					
Gymnosarda unicolor	7	4	1	1		
Cheilinus undulatus	6		1			
Coris aygula	4	1				
Epibulus insidiator	5					
Hipposcarus harid	3	1				
Scarus gibbus	18	1				
S. rubroviolaceus	3					
Acanthurus xanthopterus	2					
Balistoides viridescens	1					
Totals	346	74	53	37	11	8

analyses obtained by the author from localities other than the Marshall Islands have been included in this report. The food habit data are presented in the species accounts following the assay of toxicity.

The length measurement most often used for bony fishes was standard length (SL). This was taken from the front of the snout to the end of the hypural plate (hence base of caudal fin). When the method of measuring length is not specified, standard length is intended. Fork length (FL) was used for carangids and scombrids because scutes or keels laterally on the caudal peduncle prevent the accurate external determination of the base of the caudal fin. Total length (TL) was employed for eels, nurse sharks, and some proportional measurements. The length usually given for requiem sharks is precaudal length (PCL).

Schultz and collaborators (1953-66) was the primary reference for the identification of ciguatoxic fishes and the fishes from their stomachs. Enewetak and Bikini were among the islands from which large collections of fishes were made for this systematic work. When names other than those given by Schultz and collaborators are used, an explantion is given in the species accounts.

The species of ciguatoxic fishes which were studied are discussed in approximate phylogenetic sequence below. The results of the mongoose feeding tests are summarized in Table 1 for Enewetak and Table 2 for Bikini.

TABLE 2.—Summary of mongoose feeding tests (liver-viscera, sharks excepted) of fishes collected at Bikini (0 = nontoxic; 5 = death of test animal).

Species	Intensity of reaction					
	0	1	2	3	4	5
Carcharhinus amblyrhynchos	1					
Galeocerdo cuvier	1					
Sphyraena barracuda	1	1	1			
S. forsteri			2			
Crenimugil crenilabis	3					
Epinephelus hoedtii	1					
E. maculatus	2					
E. microdon	2	1	4	1		1
E. tauvina	1		1			
Plectropomus leopardus	1					
Variola louti	2					
Aprion virescens	7	1				
Lutjanus bohar	112	15	8	6	2	
L. gibbus	32	3				
L. monostigmus	4	1				
Lethrinus amboinensis	9					
L. kallopterus	2					
L. miniatus	12					
L. xanthochilus	2					
Caranx ignobilis	2					
C. melampygus	6					
Gymnosarda unicolor	3					
Pseudobalistes flavimarginatus	2					
Totals	208	22	16	7	2	1

RESULTS

Orectolobidae (Nurse Sharks)

Nebrius ferrugineus (Lesson) (Figure 1): Like other orectolobids, this shark has a prominent nasal barbel, relatively small mouth, the fourth and fifth gill openings over the pectoral base, and the two dorsal fins set posteriorly on the body. The teeth, which are small and in numerous rows (the first three or four functional), have a large central cusp with four to six smaller cusps on each side (the teeth of the related genus *Ginglymostoma* have an even larger central cusp and only two small cusps on each side). The two dorsal fins are of nearly equal size, the first originating slightly anterior to the origin of the pelvic fins and the second distinctly anterior to the origin of the anal fin; the caudal fin is about 30% TL.

Nebrius concolor Rüppell appears to be a junior synonym. Bass et al. (1975b) employed this name,

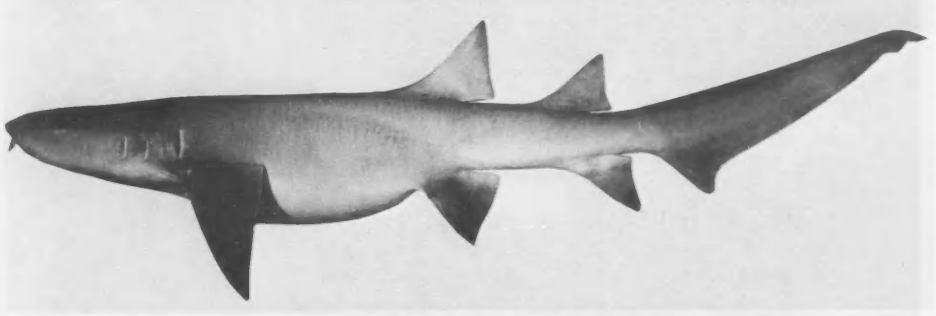

FIGURE 1.—*Nebrius ferrugineus*, 1,080 mm PCL, 1,496 mm TL, 18.1 kg, Enewetak, Marshall Islands.

but admitted that Lesson's *ferrugineus* might have priority.

This shark is a shallow-water species, usually seen at rest on the bottom during daylight hours. It is not common in the Marshall Islands. Two specimens were obtained from Enewetak, 1,400 and 1,487 mm TL, weighing 11.7 and 14.1 kg. The flesh of neither was toxic.

Fourmanoir (1961) stated that the principal food of this shark consists of octopuses and xanthid crabs. Gohar and Mazhar (1964) reported cephalopods, fishes, and parts of corals (*Stylophora*) from the stomachs of Red Sea specimens (the corals were probably accidentally ingested). Hiatt and Strasburg (1960) found a rabbitfish, *Siganus* sp., in the stomach of one of three specimens collected at Enewetak.

The stomach of the smaller of the two specimens taken during the present study contained a surgeonfish, *Acanthurus glaucopareius*, 95 mm SL. Three other Enewetak specimens and one from the Tuamotu Archipelago (to 1,615 mm TL, 20.9 kg) had empty stomachs.

Carcharhinidae (Requiem Sharks)

Carcharhinus albimarginatus (Rüppell) (Figure 2): The silvertip shark is one of three carcharhinid sharks with white on the tips of its fins; the others are the oceanic whitetip shark, *C. maou* (Lesson) (*C. longimanus* a junior synonym), and the whitetip reef shark, *Triaenodon obesus* (Rüppell). The name silvertip has been adopted by Kato et al. (1967) and others to avoid confusion with the other two species with white-tipped fins. The white on the silvertip's fins is not confined to the distal ends but continues along the posterior margins. The apex of the first dorsal fin is somewhat pointed (broadly rounded on *C. maou*); the origin of this fin is over the inner edge of the pectoral fin. The pectorals are about 18% TL (about 28% on *C. maou*). A median interdorsal ridge is present. There are usually 26 upper and 24 lower teeth. The precaudal vertebrae vary from 115 to 125.

Carcharhinus albimarginatus has not been reported as poisonous [Halstead (1967, pl. VI, fig. 3) illustrated it but misidentified the figure as *Triaenodon obesus*], but it would seem to have the potential for causing ciguatera because it preys in part on reef fishes. In the Marshall Islands it was usually seen on exposed outer reefs in water >30 m, though one individual was observed in the Enewetak lagoon in water only 2 m deep. Bass et al. (1973) summarized the depth distribution, noting records to 400 m. This species has attacked man.

The flesh of four silvertips, 933-1,650 mm PCL (15.0-73.5 kg), from Enewetak was nontoxic.

Fourmanoir (1961) reported the following wide variety of fishes from the stomachs of silvertips from Madagascar: *Promethichthys prometheus*, *Pristipomoides typus*, *Seriola songoro*, *Coris gaimard*, *Caesio coerulaureus*, *Acanthocybium solandri*, *Euthynnus pelamis*, and *Neothunnus al-*

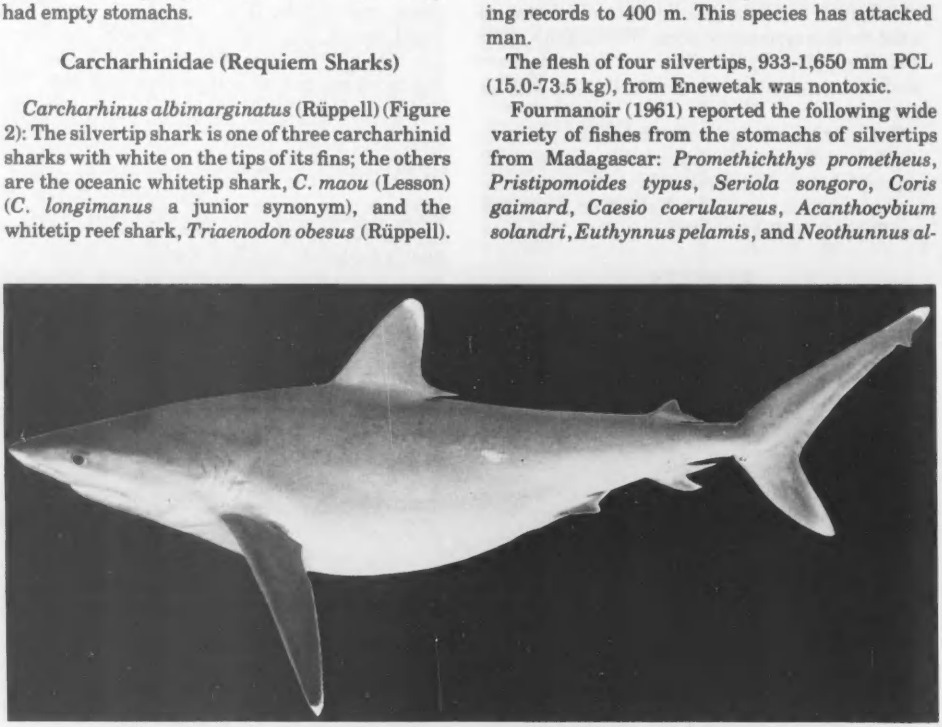

FIGURE 2.—*Carcharhinus albimarginatus*, 1,650 mm PCL, 2,154 mm TL, 73.5 kg, Enewetak, Marshall Islands.

bacora (= *Thunnus albacares*). Bass et al. (1973) examined the stomach contents of 10 specimens of *C. albimarginatus* from the western Indian Ocean. They found teleost fishes (exocoetid, myctophid, several soleids) in seven sharks; a spotted eagle ray, *Aetobatis narinari*, in one; and an octopus in one.

The stomach of one of the Enewetak silvertips (1,240 mm PCL, 1,650 mm TL) contained a gray reef shark, *Carcharhinus amblyrhynchos*, 483 mm PCL and 616 mm TL, as well as the dental plates and pharyngeal mills of three parrotfishes (*Scarus*). The stomachs of the other three sharks were empty.

Carcharhinus amblyrhynchos (Bleeker) Figure 3): This shark, now popularly known as the gray reef shark, was referred to by Schultz in Schultz and collaborators (1953) as *Carcharhinus menisorrah* (Müller and Henle). Bass et al. (1973) and Garrick (in press) are followed in the use of the name *C. amblyrhynchos* herein.

The gray reef shark lacks dark pigment distally on the first dorsal fin, but the tips of the other fins are broadly blackish, and there is a broad black margin posteriorly on the caudal fin. The dark markings on the fins are more evident on live than on dead specimens. The origin of the first dorsal fin is over the pectoral axil or anterior part of the inner edge of the pectoral fin. A short interdorsal ridge is present or absent. There are 26-28 upper teeth and 24-26 lower teeth; the precaudal vertebrae vary from 110 to 117 (two Enewetak specimens had 117).

This shark is abundant in the Marshall Islands. It occurs in many habitats from lagoons to ocean reefs, but it is most commonly encountered in deep channels and outer reef areas. It does not penetrate the shallows as readily as *C. melanopterus*.

The flesh of 11 specimens from Enewetak, 1,017-1,190 mm PCL (17.2-26.3 kg), and 1 from Bikini (3.6 kg, length not taken) was tested. All gave a zero reaction for ciguatoxin. The viscera of one of these, 1,158 mm PCL, from Enewetak produced a reaction of 2, however.

The stomachs of 74 individuals, 520-1,230 mm PCL (2.7-32.4 kg), from Enewetak, Fanning and Palmyra in the Line Islands, Marcus Island, Johnston Island, Palau Islands, and Ducie and Henderson in the Pitcairn Group, were examined for food. Forty-nine stomachs were empty or contained only bait. Three had eaten cephalopods (two octopus, one squid), and the rest contained the remains of fishes (in some cases only the lens of an eye or a few remnants of spines or bones). The fishes that could be identified to family or genus were the following: muraenid, belonid, exocoetid, *Fistularia*, *Decapterus*, *Trachinotus*, *Acanthurus*, and another acanthurid (either *Acanthurus* or *Ctenochaetus*).

In spite of its relatively small size, the gray reef shark constituted a hazard to the personnel of the survey program, particularly when divers were spearfishing or collecting with rotenone. Several

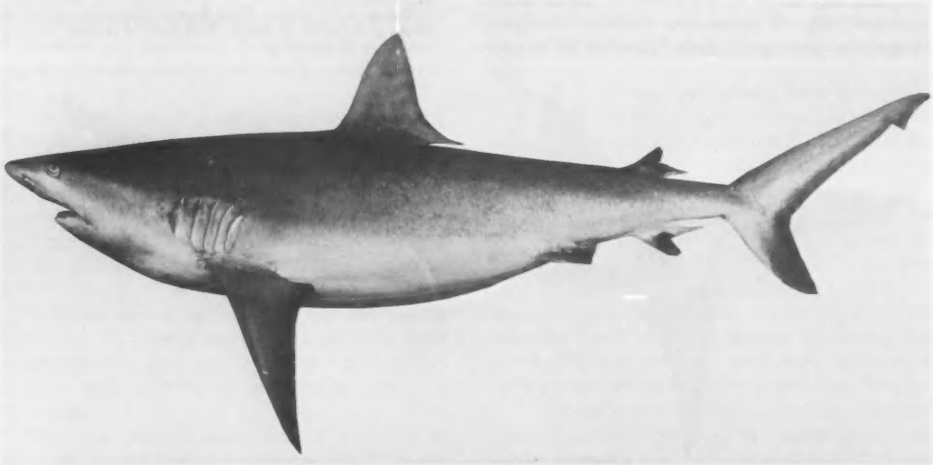

FIGURE 3.—*Carcharhinus amblyrhynchos*, 1,288 mm PCL, 1,640 mm TL, Tahiti, Society Islands.

of these sharks were killed by powerheads when their aggressive behavior and proximity warranted. On 12 July 1975 the companion diver of the author, Russell E. Miller, sustained 7 gashes in his head requiring 25 stitches as the result of an attack by a *C. amblyrhynchos* of about 1,500 mm TL. The shark first exhibited threat posturing (see Johnson and Nelson 1973) at the back of the author. Miller sounded a warning by rapping on his scuba tank with his powerhead handle. The shark immediately turned and swam toward him, repeating the exaggerated sinuous swimming of its threat behavior as it approached. Miller struck the shark with his powerhead but the shell misfired. The shark came on to slash his head (and cut the rubber strap of his face mask) with its upper jaw. On another occasion Gordon W. Tribble had the end of his speargun seized by a gray reef shark and vigorously shaken.

Richard C. Wass (1971) has made a comparative study of the biology of the gray reef shark and the sandbar shark in the Hawaiian Islands.

Carcharhinus galapagensis (Snodgrass and Heller) (Figure 4): This shark is circumtropical in distribution, but as noted by Garrick (1967), it shows a preference for the sea around oceanic islands.

The Galapagos shark has no distinctive markings; it is dark gray dorsally, pale ventrally. The origin of the first dorsal fin is anterior to the inner free corner of the pectoral fin. The second dorsal fin is relatively large for a *Carcharhinus*, its height 2.4-2.8% TL. A distinctive median interdorsal ridge is present on the back. There are 26-30 upper teeth (the anterior upper teeth broadly triangular) and 26-29 lower teeth. The precaudal vertebrae range from 103 to 109.

A single specimen, 1,831 mm PCL, 2,426 mm TL, 41.2 kg, was collected at Enewetak. Its flesh was nontoxic.

Tester[7] examined the stomach contents of 41 Galapagos sharks caught from the Hawaiian Islands; 51% were empty. Sixty percent of the sharks had eaten bony fishes, 35% cephalopods, 20% sharks and rays, and 10% crustaceans. He commented that the larger individuals (maximum length estimated as 10 ft or 3,048 mm) fed mostly on larger fishes which were torn into chunks. He regarded it as a dangerous species; Randall (1963) documented a fatal attack.

Bass et al. (1973) found food in 18 of 22 individuals of this species; 12 of the stomachs contained teleost fishes (serranid, *Platycephalus*, and a flatfish) and 10 had squids or octopuses (plus the shell of a bivalve mollusk).

The Enewetak specimen was empty as were three others 1,460-1,690 mm PCL from the Pitcairn Group. One of 1,580 mm PCL from Rapa contained the head of an unidentified eel.

Carcharhinus limbatus (Valenciennes) (Figure 5): The shark occurs in the Atlantic as well as the Indo-West Pacific. In the Atlantic it bears the common name of blacktip shark, a name which is poor for the species in the Pacific for two reasons.

[7]Tester, A. L. 1969. Final Report, Cooperative Shark Research and Control Program, University of Hawaii. Mimeogr. Rep., 47 + 36 append. p.

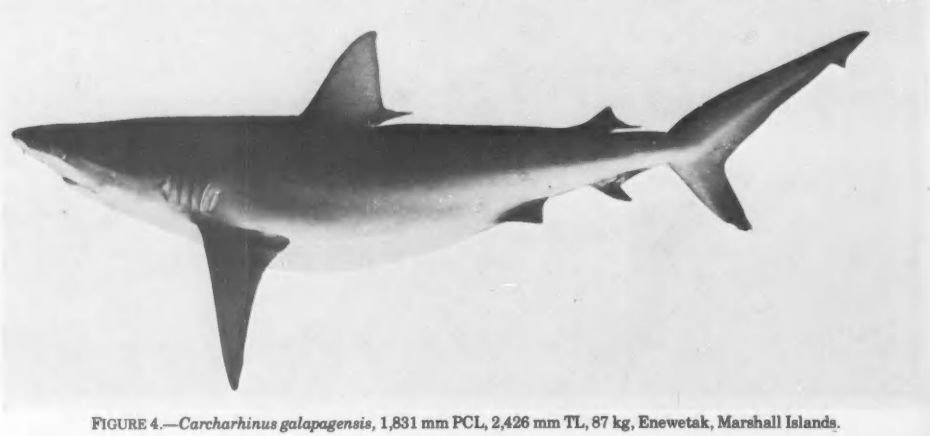

FIGURE 4.—*Carcharhinus galapagensis*, 1,831 mm PCL, 2,426 mm TL, 87 kg, Enewetak, Marshall Islands.

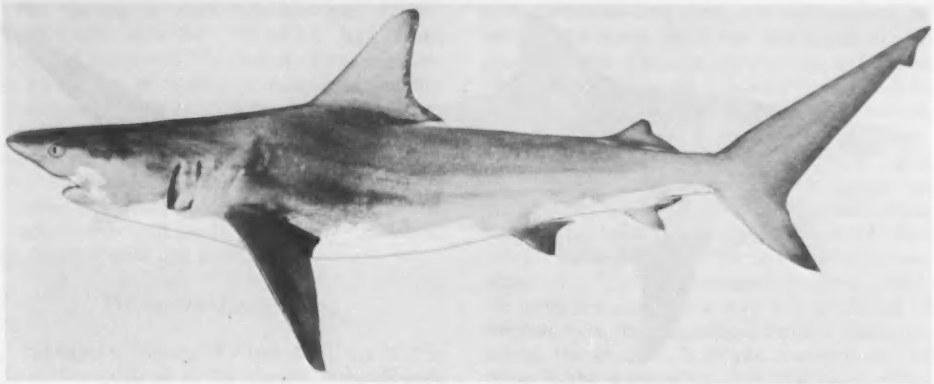

FIGURE 5.—*Carcharhinus limbatus*, 1,415 mm PCL, 1,910 mm TL, 38.2 kg, Enewetak, Marshall Islands.

The tips of the fins of Pacific individuals, particularly adults, are only slightly tipped or edged in black. Also the common Indo-West Pacific *C. melanopterus* has very pronounced black tips on its fins (see Randall and Helfman 1973, fig. 1, 2). To avoid confusion in common names, *C. melanopterus* has been referred to by many recent authors as the blacktip reef shark (though Bass et al. 1973, call it the blackfin reef shark).

Carcharhinus limbatus is distinctive in lacking a median ridge on the back between the dorsal fins, having a relatively long snout, and the cusp of its teeth notably narrow and erect. It has 29-32 upper, 28-32 lower teeth, and 88-102 precaudal vertebrae. The color is gray to bronze on the back, white below, with a long band of the dark dorsal color extending posteriorly from the last gill opening into the pale ventral color as far as the pelvic fins.

Two individuals of *C. limbatus* were caught at Enewetak during the ciguatera survey; these constitute the first records of the species from the Marshall Islands. The head of the illustrated specimen (which was 1,415 mm PCL, 1,910 mm TL, and weighed 38 kg) has been preserved in the Bernice P. Bishop Museum under catalog number 18074.

Only the second specimen, which was about 1,700 mm PCL (original data sheet with measurements was lost), was tested for toxicity. The viscera gave a reaction of 2 when fed to a mongoose.

Bass et al. (1973) reported on 55 of 101 sharks of this species with food in their stomachs. Fifty-one of the sharks had eaten teleost fishes, including: *Scomberomorus commerson*, *S. leopardus*, *Pomadasys* sp., *Sarpa salpa*, *Johnius hololepidosus*, *Leiognathus equula*, *Elops saurus*, *Tilapia mossambica*, and a soleid. Six contained elasmobranchs, including a small *C. obscurus* and a *Rhinobatus annulatus*. Two had eaten *Sepia* sp., and one a spiny lobster, *Panulirus homarus*.

The two Enewetak specimens had empty stomachs.

Galeocerdo cuvier (Peron and Lesueur) (Figure 6): The circumtropical tiger shark is readily identified by its broad bluntly rounded snout, distinctive teeth (heavily serrate, convex on the medial margin, and deeply notched on the lateral), low longitudinal keel on the side of the caudal peduncle, and dark bars (though these tend to fade with age).

The flesh of two tiger sharks from Enewetak, 1,770 and 2,410 PCL (72 and 174 kg), and one from Bikini, 1,498 mm PCL, was tested. None of these sharks were toxic. The Bikini specimen was caught at 4:30 a.m. in only 1.7 m of water.

Bigelow and Schroeder (1948) summarized the literature on food habits, danger to man, etc., of this shark. Other authors such as Clark and von Schmidt (1965), Bass et al. (1975a), and Tester (see footnote 7), have added to the list of the great variety of marine animals (mainly fishes) that this species will take as food, as well as sundry items of garbage and refuse discarded into the sea by man.

The stomach of the largest of the Marshall Islands specimens contained the scutes of a green turtle, *Chelonia mydas*, estimated to be 500 mm carapace length and the bait (a gray reef shark).

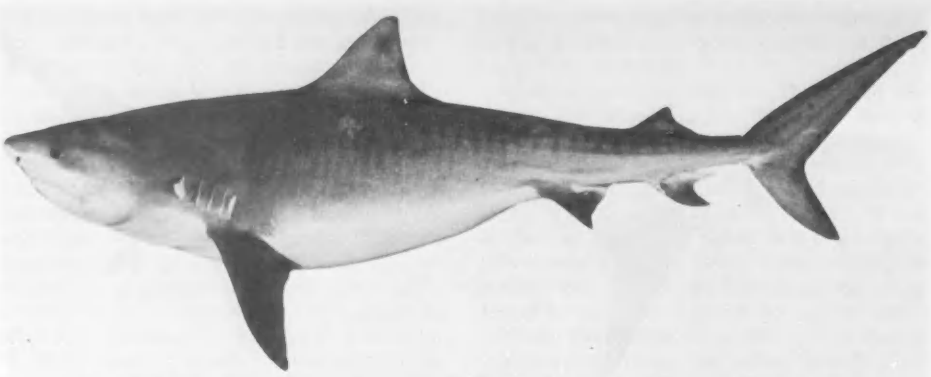

FIGURE 6.—*Galeocerdo cuvier*, 2,410 mm PCL, 3,055 mm TL, 175 kg, Enewetak, Marshall Islands.

The stomachs of the other two sharks were empty. Three other tiger sharks from Enewetak had food in their stomachs. One of 3,150 mm TL contained shark vertebrae. The second of 3,581 mm TL had the scutes of a green turtle and bird feathers. The third, 3,048 mm TL, was filled with pieces of a porpoise and the digested remains of shark fins.

A tiger shark of 3,327 mm TL from Ua Huka, Marquesas Islands, was empty, as was one of 2,895 mm TL from Oahu. Another from Oahu of 3,048 mm had an extremly distended stomach filled with heads of skipjack tuna (neatly cut by a knife, hence probably discarded from a fishing boat), plastic bags of garbage and aluminum foil, a cat, and two small reef fishes (one a balistid). It also contained the bait (the head of a calf). A 3,100 mm specimem weighing 174.6 kg taken by a set line at night at Rapa had eaten parts of a tiger shark larger than itself (probably from an individual caught on another hook), as well as a seabird.

Triaenodon obesus (Rüppell) (Figure 7): The whitetip reef shark, once classified by most ichthyologists in the family Triakidae, is now recorded as a carcharhinid (Compagno 1973). In spite of its scientific name, it is rather slender compared with most species of the family. Apart from its slim form and white-tipped first dorsal fin and upper caudal lobe, *T. obesus* is distinctive in its very blunt snout and teeth which bear a small cusp on each side of the main central one. It is widespread throughout the tropical and subtropical Indo-West Pacific region and ranges to the eastern Pacific as well. Banner and Helfrich (1964) and Brock et al. (1965) have reported this species as poisonous from Johnston Island.

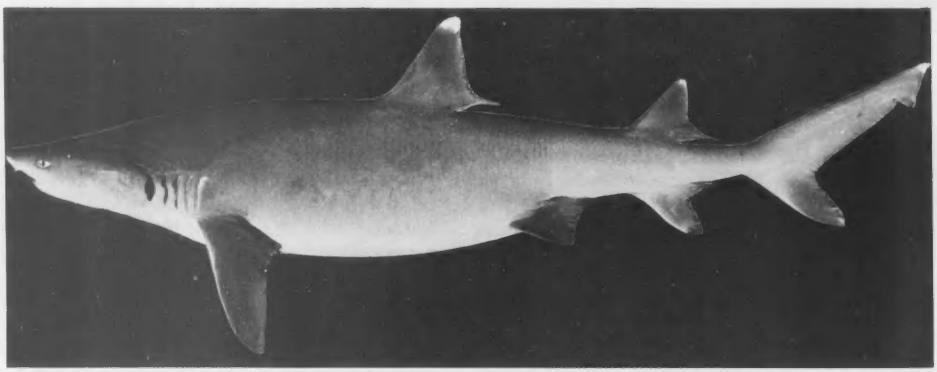

FIGURE 7.—*Triaenodon obesus*, 1,218 mm PCL, 1,520 mm TL, 23.5 kg, Tahiti, Society Islands.

The toxicity of eight whitetip reef sharks, 1,003-1,183 mm PCL (8.4-22.4 kg), from Enewetak was tested. The flesh of all was negative for ciguatoxin by feeding to mongooses, but the viscera of two gave positive reactions of 1.

Randall (1977) studied the biology of this species. He opened the stomachs of 56 specimens (24 of which were from Enewetak): 33 were empty, 6 had eaten octopuses (2 of these also contained fishes), and the rest had the remains of reef fishes, especially scarids and acanthurids.

Dasyatidae (Sting Rays)

Taeniura melanospilos Bleeker (Figure 8): The specimens collected in the Marshall Islands were initially called *Taeniura brocki* Schultz. However, it now seems more likely that they should be identified as *T. melanospilos* Bleeker. Schultz in Schultz and collaborators (1953) differentiated *T. brocki* by its having the venomous spine inserted "...at about half length of tail..." in contrast to a little behind the first third on *T. melanospilos*, in having the snout contained five times in the greatest width of the disc (given as six by Bleeker for *T. melanospilos*), and in having "...very numerous irregularly shaped small brownish to blackish spots and blotches speckling dorsal surface of disk ...," as opposed to "... numerous rounded black spots ..." for *T. melanospilos*. After noting the measurements of the position of the spine and the length of the tail of his only specimens of *T. brocki*, Schultz wrote, "...end of the tail may have been bitten off...." On the specimen illustrated herein, the spine is inserted at a point 41% the length of the tail from the base. From Schultz' measurements, the snout of *T. brocki* is contained 5.14 times in the width of the disc. The snout of the specimen illustrated herein is contained about 5.3 times in the disc width. Without knowledge of variation of this character and perhaps proportional differences with growth, the differentiation of species on this magnitude of snout length is questionable. Furthermore, Bleeker's (1853) de-

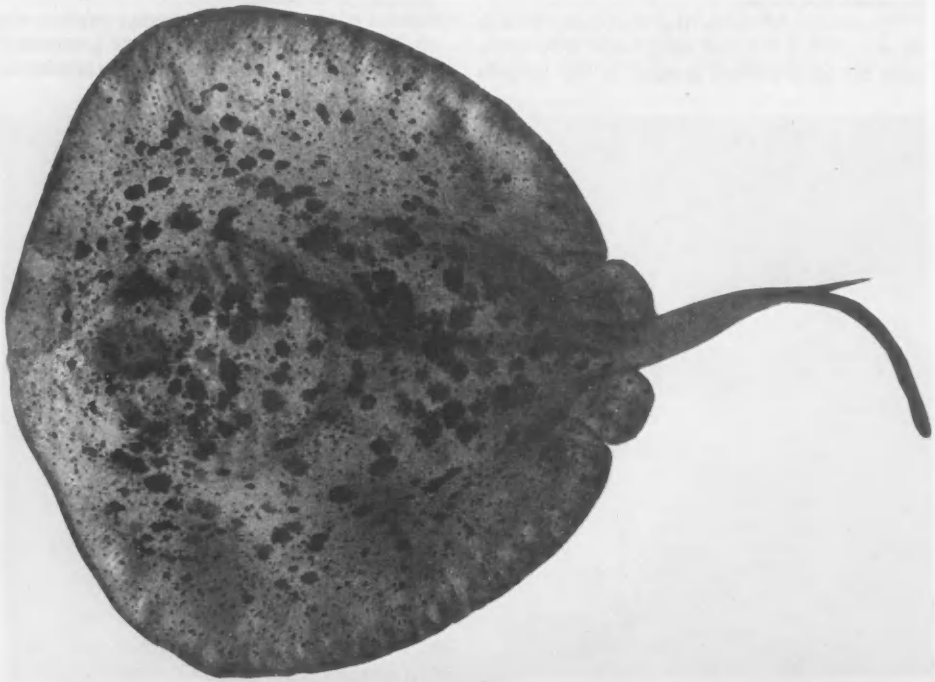

FIGURE 8.—*Taeniura melanospilos*, 1,255 mm disc length, 2,008 mm TL, 69 kg, Enewetak, Marshall Islands.

scription of the dark spots of *T. melanospilos* was not simply round as Schultz stated, but round and oblong and variably small, medium, and large.

One stingray of this species from Enewetak with a disc length of 870 mm (disc width 950 mm; tail length 950 mm), weighing 19.05 kg, was tested. It was not poisonous.

The stomach of this ray was empty. Another of 1,255 mm disc length weighing 68.9 kg collected by the author at Enewetak in 1968 had eaten two labrid fishes (*Xyrichtys*) and a parrotfish, *Scarus* sp. It was a female with seven embryos.

Muraenidae (Morays)

Lycodontis javanicus (Bleeker) (Figure 9): This moray is brown with large dark blotches and numerous small dark spots; the gill opening is in a large black spot; there are no pale margins on the fins. It is probably the species of eel reported by Khlentzos (1950) which poisoned 57 Filipino laborers at Saipan, Mariana Islands. In spite of prompt gastric lavage, 14 of these men became comatose and 2 died.

The severity of illness from the consumption of moray eels led Halstead and Lively (1954) to regard this as a distinct category of fish toxemia which they termed "Gymnothorax poisoning." However, it appears to be principally an acute form of ciguatera, though there is a possibility of involvement of one or more other toxins.

Lycodontis javanicus is not common in the Marshall Islands, but it is abundant (for a large carnivore) at Johnston Island; in recent years it has served as the primary source of ciguatoxin for biochemical and pharmacological study at the University of Hawaii by a team of scientists headed by A. H. Banner.

Nine specimens from Enewetak measuring 1,086-1,540 mm TL and weighing 3.6-13.0 kg were tested. All were toxic, two at the 2 level, one at 3, three at 4, and three at 5 from the feeding of liver and viscera to mongooses. The flesh of two of these eels with a mongoose reaction of 4 was tested; one was a 1 and the other a 2. One of the eels with a mongoose test of 5 for liver-viscera gave a reaction of 3 with flesh.

Brock (1972) studied some aspects of the biology of *L. javanicus*, including an analysis of the toxicity at Johnston Island. Of 1,074 specimens, only 158 (14.7%) contained food; 88.8% of the stomach-content material consisted of fishes (representing 17 different families, the Scaridae predominating). Among the more interesting prey species was

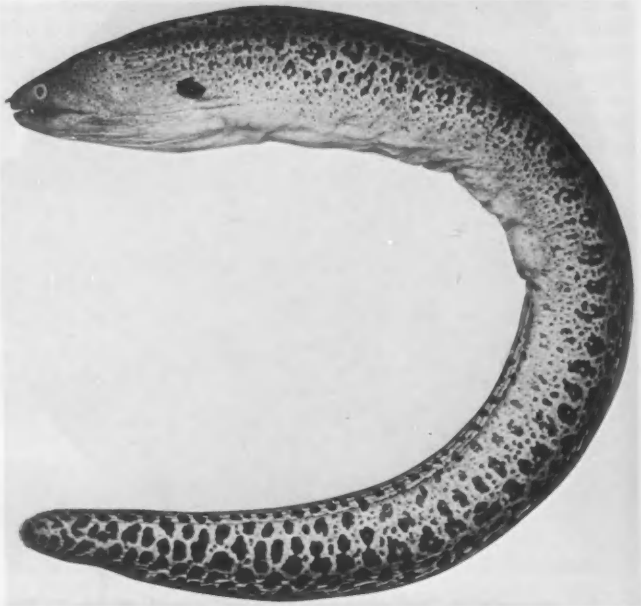

FIGURE 9.—*Lycodontis javanicus*, 732 mm TL, Enewetak, Marshall Islands.

a whitetip reef shark 465 mm PCL, taken from the stomach of a 1,422 mm moray. Octopus and spiny lobster were also eaten.

This is the largest species of moray in the Indo-Pacific region. Schultz (1949) attributed an attack on the late Vernon E. Brock at Johnston Island by a moray of about 10 ft (3,048 mm) in length to be *Enchelynassa canina*. Following a later interview with Brock, Randall (1969) reported that the eel was actually *L. javanicus* and the length 7-8 ft (2,134-2,438 mm). Stephens (1963) noted that the largest moray measured at Johnston during his stay at the island to be 7 ft 10 in (2,388 mm). The author tended to disbelieve occasional reports by divers of individual *L. javanicus* of 10-12 ft (3,048-3,658 mm) until he observed one of an estimated 3,000 mm long off Mafia Island, Tanzania, which was flushed from a cave with rotenone (the eel recovered from the affect of the rotenone and returned to its cave).

The stomach contents of 11 specimens 417-1,905 mm TL (the largest weighed 24.5 kg) were examined during the present study. Six of these eels were from Enewetak, the rest from Oeno, Pitcairn, Johnston, and Truk. Four had empty stomachs. The smallest contained a crab chela. The others had eaten fishes (two contained *Scarus* sp., one *Diodon* sp., and another *Thalassoma purpureum*). The stomach of a 1,540 mm, 13 kg specimen was distended with *Kyphosus cinerascens*, *Acanthurus nigricauda* (identified as *A. nigricans* by Schultz and Woods in Schultz and collaborators 1953, and as *A. gahhm* by Randall 1956), and *A. nigroris*, all of which totalled 1.5 kg. These fishes must be discounted as normal prey, however, as they were undoubtedly eaten as a result of a dynamite station at the Enewetak garbage pier. The eel was collected with a powerhead blast immediately after the dynamite explosion when it was discovered within the area in which many other fishes had just been killed.

Holocentridae (Squirrelfishes)

Adioryx spinifer (Forsskål) (Figure 10): The largest of the squirrelfishes, this species exceeds 300 mm SL. It has a deep body, the depth about 2.5-2.7 in SL, projecting lower jaw, 40-44 lateral line scales, and a well-developed venomous spine at the corner of the preopercle. The color is red and silvery with a deep red spot behind the eye and another on the pectoral axil; the fins are yellow except the spinous dorsal which is deep red. Described from the Red Sea, the species has since

FIGURE 10.—*Adioryx spinifer*, 260 mm SL, Enewetak, Marshall Islands.

been recorded from throughout the tropical Indo-West Pacific. It is often found in caves.

Randall (1958) reported this species as occasionally toxic in Tahiti. In his review of ciguatoxic fishes, Halstead (1967) cited this and three other references.

Six specimens, 232-280 mm SL (0.35-0.66 kg), were collected for assay of toxicity from Enewetak. All were nontoxic.

Randall (1958) found fishes in the stomachs of two adults from Tahiti. Hiatt and Strasburg (1960) examined the stomachs of nine from Enewetak, one of which was empty. Crabs (especially xanthids) dominated the stomach contents of the other specimens: 12% contained stomatopods and 12% fishes. The stomachs of five specimens from Hawaii reported by Hobson (1974) contained crustaceans, mainly caridean shrimps, and xanthid crabs.

For this food-habit study a total of 31 specimens ranging from 182 to 280 mm SL were obtained, principally from Enewetak, but a few from the Red Sea, Society Islands, Hawaiian Islands, and American Samoa. Because this species is nocturnal, like other holocentrids in general, most specimens were collected in early morning hours. Twenty-eight of these fish had food in their stomachs; 82% by volume consisted of crabs, mostly xanthids, 5% fishes (including *Lycodontis rueppelliae* and a prejuvenile acanthurid), and the rest shrimps, a hermit crab, unidentified crustaceans (mostly larval), larval mollusks, and an unidentified worm.

Sphyraenidae (Barracudas)

Sphyraena barracudaa (Walbaum) (Figure 11): The great barracuda is distinctive in having a few blackish blotches on the side, especially posteriorly and ventrally, and the lowest lateral line scale count of the genus (76-85). It is the worst offender for causing ciguatera in the West Indies, due not only to the high level of toxicity of occasional individuals but also to its relative abundance there. The species is far less common in the Indo-West Pacific.

Seven specimens 563-1,182 mm SL (1.5-13.6 kg) from Enewetak were tested, and three from Bikini, 640-1,143 mm SL, the largest 15.0 kg. Three from Enewetak were nontoxic, one was toxic at the level of 1; two gave a reaction of 2; and one (1,050 mm, 12.7 kg) was a 3. The three from Bikini were tested at 0, 1, and 2.

de Sylva (1963) made a study of the systematics and life history of the great barracuda, principally from material from the western Atlantic. He reviewed previous papers which presented limited data on the food habits of this species. Among them was the report by Ommanney in Wheeler and Ommanney (1953) on the fishes found in the stomachs of 5 of 12 specimens of *S. commersoni* (now known to be a junior synonym of *S. barracuda*) from the Seychelles. One of the five contained an unidentified eel and another *Lethrinus ramak*. de Sylva mistakenly reported Ommanney's five barracuda as all having eaten *L. ramak*.

de Sylva opened the stomachs of 901 great barracuda, including juveniles, from various localities in the tropical western Atlantic. Of these, 529 (58.7%) contained food. Fishes were found in 82.2% of the stomachs, plant material in 2.8% (probably accidentally ingested with prey), invertebrates (notably squids and shrimps) in 2.6%, and unidentifiable material in 12.2%. The Hemiramphidae was the most common family of fishes found in the stomachs of 446 adult barracuda from Florida, whereas tetraodontid fishes predominated in the stomach contents of 132 adults from Bimini, Bahamas.

The stomachs of 13 specimens, 560-1,182 mm

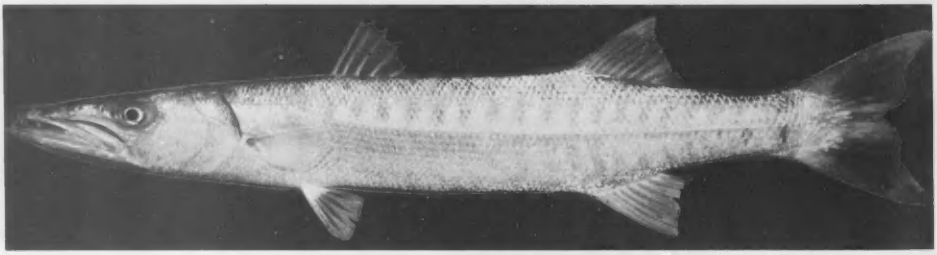

FIGURE 11.—*Sphyraena barracuda*, 524 mm SL, Palmyra, Line Islands.

SL, from the Marshall Islands and Line Islands were examined during the present study. Nine of these fishes had empty stomachs. The rest contained the remains of fishes.

Sphyraena forsteri Cuvier (Figure 12): This barracuda is readily distinguished from all others by its large eye, black blotch in the axil of the pectoral fins, and spiniferous plates on its first gill arch instead of gill rakers or no trace of rakers at all.

de Sylva (1973:18) wrote that this species of barracuda has been implicated in poisoning but added that the examples appear to be misidentifications of *S. barracuda*. Hiyama (1943, pl. 3, fig. 9), however, did not confuse his specimens with *S. barracuda*. He reported *S. forsteri* from the Marshall Islands as slightly poisonous from feeding flesh to cats and mice.

Only two individuals of this species were caught during the survey, both from Bikini and both the same size (610 mm SL, 1.8 kg). Each produced a toxic reaction of 2.

The stomach of one of these fish contained fish remains; the other was empty.

Mugilidae (Mullets)

Crenimugil crenilabis (Forsskål) (Figure 13): This large mullet has a deeply emarginate caudal fin, a black spot at upper pectoral base, and 37-39 rows of scales between the gill opening and the caudal base. Widespread in the tropical Indo-West Pacific region, it is usually seen in small aggregations in the shallows of lagoons and on outer reef flats. It appears to feed on fine algae and detritus from the substratum. After feeding on a sandy bottom it has been observed to expel sand from its gill openings. The spawning by a large school at the surface at night in the Enewetak lagoon was described by Helfrich and Allen (1975). *Crenimugil crenilabis* has been reported as poisonous by Randall (1958) from the Society Islands. It is probably the species of mullet that Ross (1947)

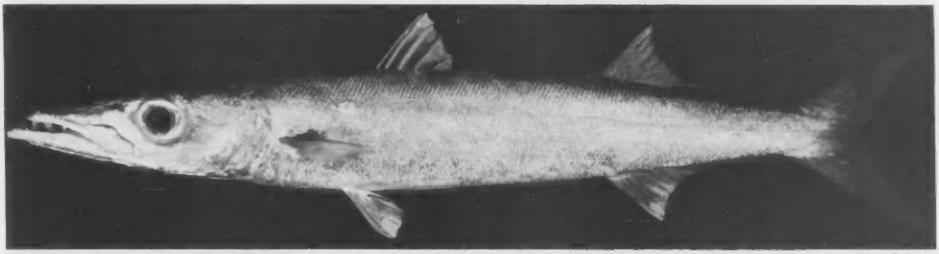

FIGURE 12.—*Sphyraena forsteri*, 540 mm SL, 1.2 kg, Enewetak, Marshall Islands.

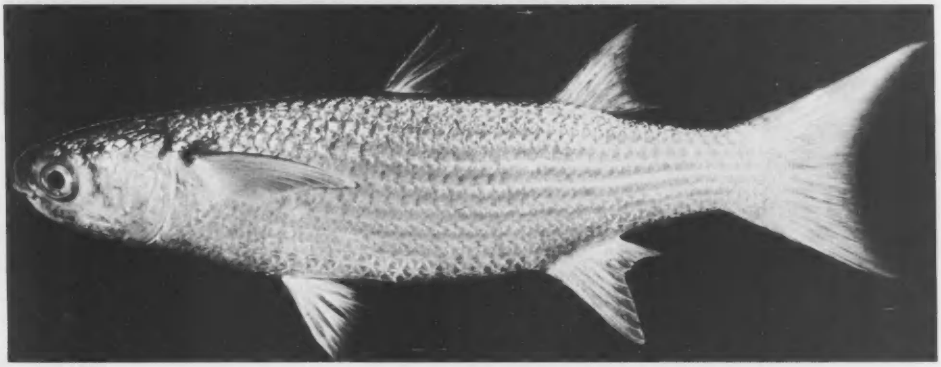

FIGURE 13.—*Crenimugil crenilabis*, 337 mm SL, Enewetak, Marshall Islands.

found toxic at Fanning, Line Islands (Randall 1958).

Three specimens, 248-406 mm (0.4-0.7 kg), were obtained for testing from Bikini. None were toxic.

Serranidae (Groupers)

Cephalopholis argus Bloch and Schneider (Figure 14): This common brown blue-spotted grouper has 9 dorsal spines (in contrast to 11 for the groupers of the genus *Epinephelus*). It does not reach large size, but is has occasionally been implicated in ciguatera. Although it is most abundant in outer reef areas, it also occurs on lagoon reefs.

A total of nine specimens from Enewetak were tested; these ranged from 278 to 390 SL (0.45-1.6 kg). Two were nontoxic, three gave a reaction of 1, three were recorded as 2, and the largest was a 4.

Randall (1958a) found 8 of 10 individuals of this grouper from the Gilbert Islands with empty stomachs; 1 had eaten a fish (probably from rotenone), and 1 a penaeid shrimp. Randall and Brock (1960) obtained 280 specimens for food-habit study, of which 182 were empty; 77.5% contained fishes and the rest crustaceans. Hiatt and Strasburg (1960) reported on food in five of eight stomachs from the Marshall Islands as crustaceans, fishes, and polychaetes. Helfrich et al. (1968) examined the stomachs of 51 from Palmyra; they found fishes in 89% of the stomachs and crustaceans. Harmelin-Vivien and Bouchon (1976) caught 43 *C. argus* for stomach-content analyses in Madagascar. They found fishes 95.7% by weight, shrimps 3.9%, and stomatopods 0.4% in the stomachs.

For the present study the stomachs of 39 specimens, 145-392 mm SL, from Enewetak, Society Islands, Samoa Islands, Palmyra, Marcus Island, and Pitcairn, were examined. Twenty-six were empty, one had eaten a stomatopod, and the rest contained fishes (two of these were the acronurus stage of Acanthuridae, one a labrid, one an antennariid, and one *Apogon kallopterus*).

Epinephelus fuscoguttatus (Forsskål) (Figure 15): The name *E. fuscoguttatus* was used by Schultz in Schultz and collaborators (1953) for the more common related species properly called *E. microdon* (Bleeker) (systematic clarification by Randall 1964). The two are similar in morphology and color. *Epinephelus fuscoguttatus* has higher pectoral ray counts (18 or 19, compared with 16 or 17 for *E. microdon*) and more lower limb gill rakers (18-21, including rudiments, compared with 16 or 17 for *E. microdon*).

This grouper is a large species; it is not common. Furthermore, it is the most wary of Marshall Islands groupers. Seven specimens (335-780 mm SL, 3.1-15.4 kg) were taken at Enewetak for testing, and none at Bikini. Four of the seven were toxic at the 2 level, and one (710 mm SL) was a 3.

Harmelin-Vivien and Bouchon (1976) caught four individuals of this species for food-habit study in Madagascar. The stomachs contained 94.2% fishes by weight and 5.8% brachyuran crabs.

The stomachs of seven specimens from

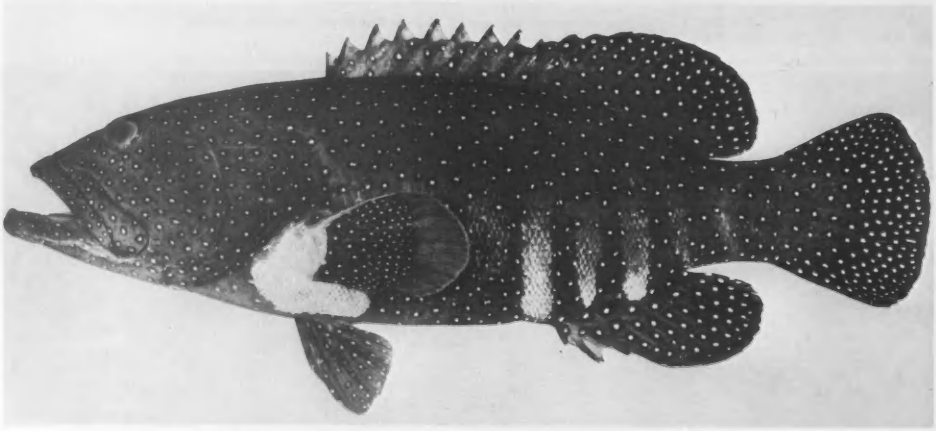

FIGURE 14.—*Cephalopholis argus*, 232 mm SL, Tahiti, Society Islands.

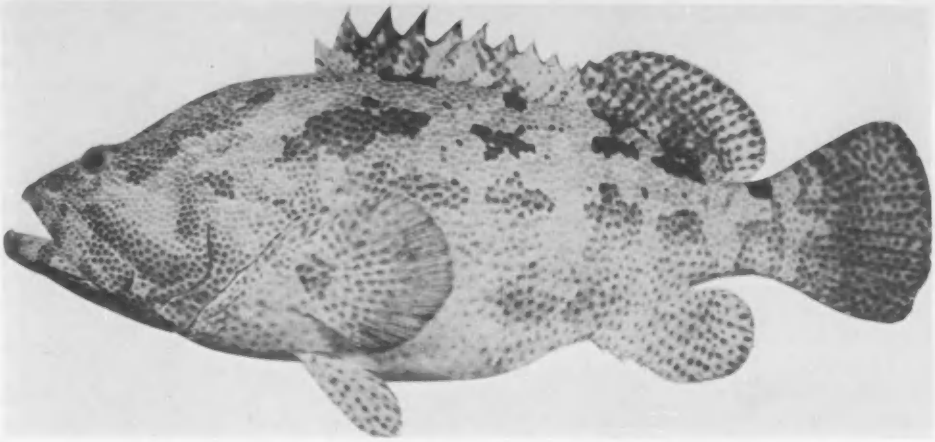

FIGURE 15.—*Epinephelus fuscoguttatus*, 551 mm SL, 5.9 kg, Gulf of Aqaba, Red Sea.

Enewetak were examined. Four were empty, one had an octopus, one had fish remains, and the last contained unidentified tissue which appeared to be cephalopod in origin. A specimen 408 mm SL from the Red Sea had crab remains in its stomach.

Epinephelus hoedtii (Bleeker) (Figure 16): Schultz in Schultz and collaborators (1953) described this fish as new from the Marshall Islands, naming it *E. kohleri*. It is relatively deep bodied and has a slightly emarginate to truncate caudal fin. He differentiated it from "... all of the 'varieties' of *flavocaeruleus* described by Boulenger in having the body spotted with dark blotches in addition to tiny dark specks." Although more study is needed of the complex of forms which Boulenger

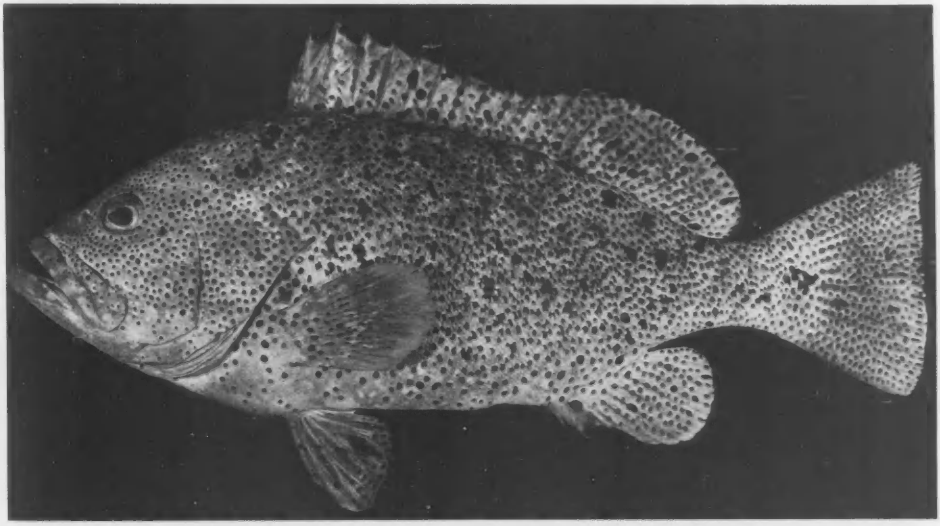

FIGURE 16.—*Epinephelus hoedtii*, 319 mm SL, Enewetak, Marshall Islands.

(1895) regarded as varieties of *flavocaeruleus*, I believe that the variety called *E. hoedtii* (Bleeker) is a valid species and that Schultz' *E. kohleri* is a junior synonym of it. Adult specimens, such as the type of *E. kohleri*, have the dark blotches, whereas smaller individuals, such as Bleeker's specimens, lack them. Hiyama (1943:81, pl. 18, fig. 49) identified it as *Serranus flavocaeruleus* (Lacepède).

This grouper was found around isolated coral heads in the lagoon of Enewetak. Eleven specimens, 348-429 mm SL, 1.36-2.72 kg, were tested. Six were nontoxic, three gave reactions of 1, one was a 2, and one (400 mm SL) a 4. A single specimen (2 kg) from Bikini was nontoxic.

Hiatt and Strasburg (1960) found fish fragments in the stomach of one of two specimens from the Marshall Islands.

The stomachs of the 11 Enewetak specimens were opened. Five were empty, one (429 mm SL) contained a 520 mm snake eel, *Leiuranus semicinctus*; two had eaten calappid crabs; and the remaining three contained the digested remains of fishes.

Epinephelus maculatus (Bloch) (Figure 17): This dark-spotted grouper was identified as *E. medurensis* (Günther) by Schultz in Schultz and collaborators (1953). It has also been called *E. fario* (Thunberg) by some authors. The oldest valid name, however, is *E. maculatus* (Bloch). Though the author ascertained that the type-specimen is no longer extant, Bloch's description and illustration match that of the juvenile of this species, particularly with reference to the large pale markings. Adults are distinctive in the rather elevated third and fourth dorsal spines; also there are two large dark areas on the dorsal fin and adjacent back which are separated by a pale area (both dark and light areas still have the profusion of small dark spots).

Like *E. hoedtii*, this species is found mainly around coral knolls in sandy stretches of atoll lagoons. Eleven specimens from Enewetak, 270-334 mm SL, 0.45-0.9 kg, were tested. Eight were nontoxic and three gave reactions of 1. Two from Bikini, 343 and 356 mm SL, were nontoxic.

The stomachs of 13 specimens from Enewetak and 2 from Bikini, 270-380 mm SL, were examined. One of 334 mm contained a portunid crab and unidentified fish remains; another of 345 mm had eaten a calappid crab (15% by volume), two microdesmid fish 78 and 86 mm SL (identified as *Gunnellichthys monostigma* by C. E. Dawson), and a digested fish; a third (308 mm SL) also contained *G. monostigma*; a fourth (288 mm SL) an octopus; and two others fish remains. The remaining nine stomachs were empty.

Epinephelus microdon (Bleeker) (Figure 18): This is a common species in the Marshall Islands for a grouper of moderate size. It is found on both

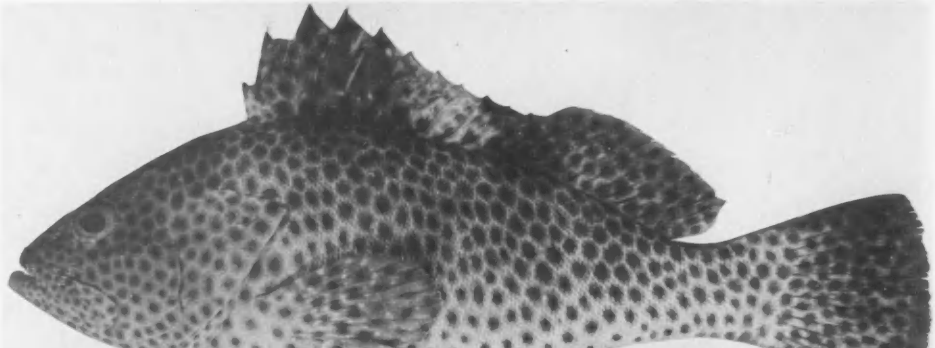

FIGURE 17.—*Epinephelus maculatus*, 280 mm SL, Enewetak, Marshall Islands.

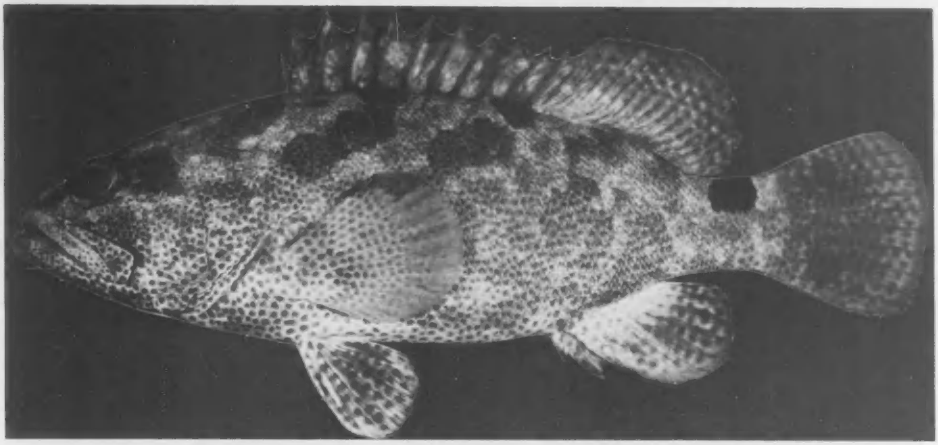

FIGURE 18.—*Epinephelus microdon*, 282 mm SL, Enewetak, Marshall Islands.

ocean and lagoon reefs. As mentioned in the account of *E. fuscoguttatus* above, it has been confused with this species by Schultz and other authors.

Thirty-nine specimens from Enewetak were tested for ciguatera toxin. These ranged from 310 to 470 mm SL and weighed 1.4-3.1 kg. Eight were nontoxic, 3 were toxic at the 1 level, 8 were 2, 13 were 3, 5 were 4, and 2 were 5 (caused death of test animals).

Nine specimens from Bikini, 279-508 mm SL, 0.9-4.1 kg, were tested. Two (279 and 342 mm) were nontoxic, one was poisonous at the 1 level, four were 2, one was 3, and one was 5 (460 mm SL).

Randall and Brock (1960) reported on the food habits of this species (as *E. fuscoguttatus*) from 33 specimens taken in the Society Islands and Tuamotu Archipelago. Of 10 with food in their stomachs, 5 had eaten crustaceans (mainly crabs) and 5 of them fishes. The eight specimens recorded by Hiatt and Strasburg (1960) as *E. fuscoguttatus* were probably *E. microdon*. Three fish had empty stomachs and the remaining five contained fishes and crustaceans.

Helfrich et al. (1968) examined the stomachs of 150 specimens from the Line Islands of which 81 contained food, mainly fishes and crustaceans. The latter accounted for 64% of the total by volume (portunid crabs and scyllarid lobsters were the most frequently recorded). A few of the groupers had eaten gastropods and cephalopods.

For the present food-habit study 44 specimens (210-610 mm SL) were examined, of which 28 were from Enewetak. The remaining 15 were from Palmyra, Tutuila, and Rapa (where the largest specimen was taken). Thirty of the 44 groupers had empty stomachs. Eight contained crabs (mainly porcellanids and portunids; one had eaten the xanthid *Carpilius convexus*), three contained fishes (one identified as *Scarus*), two had eaten octopus, and one a spiny lobster, *Panulirus*.

Epinephelus socialis (Günther) (Figure 19): This grouper has numerous small dark brown spots which tend to coalesce to form irregular longitudinal bands, especially posteriorly. The caudal fin and soft portions of the dorsal and anal fins have narrow pale margins and broad blackish submarginal zones. It is found mainly on the outer reef flat of the atoll environment, sometimes in surprisingly shallow and often turbulent water. Although fishes living entirely in this habitat would not be expected to be ciguatoxic, Halstead and Schall (1958) reported one specimen of this species as weakly toxic from Malden Island.

Two specimens, 354 and 360 mm SL, 1.1 and 1.6 kg, from Enewetak were tested. Both proved to be nontoxic.

The stomach contents of seven specimens from Enewetak, 235-360 mm SL, and one from Ducie Atoll, Pitcairn Group (420 mm SL, 2.3 kg) were examined. Three had eaten crabs (grapsids in two,

FIGURE 19.—*Epinephelus socialis*, 222 mm SL, Po: ape, Caroline Islands.

including *Percnon*, and the xanthid crab *Eriphia sebana* was found in the third); one of 330 mm contained an octopus (60% by volume) and a prejuvenile acanthurid fish; one of 354 mm contained an acanthurid 165 mm SL. The remaining stomachs were empty.

Epinephelus tauvina (Forsskål) (Figure 20): The name *E. tauvina* has often been applied to a huge grouper for which the name *E. lanceolatus* seems correct. Though the true *E. tauvina* can attain moderately large size (to perhaps 800 mm SL or more), it is not a giant species. Schultz in Schultz and collaborators (1953) described this fish as *E. elongatus* from the Marshall Islands, Mariana Islands, Phoenix Islands, and Samoa Islands, and Smith and Smith (1963) named it *E. salonotus* from the Seychelles. Katayama (1960) and Randall (1964) showed that *E. tauvina*, described from the Red Sea, is the senior synonym. This species may be confused with other dark-spotted groupers such as *E. merra* Bloch and *E. hexagonus* (Bloch and Schneider), particularly when it is small. It is differentiated from them in having 15 instead of

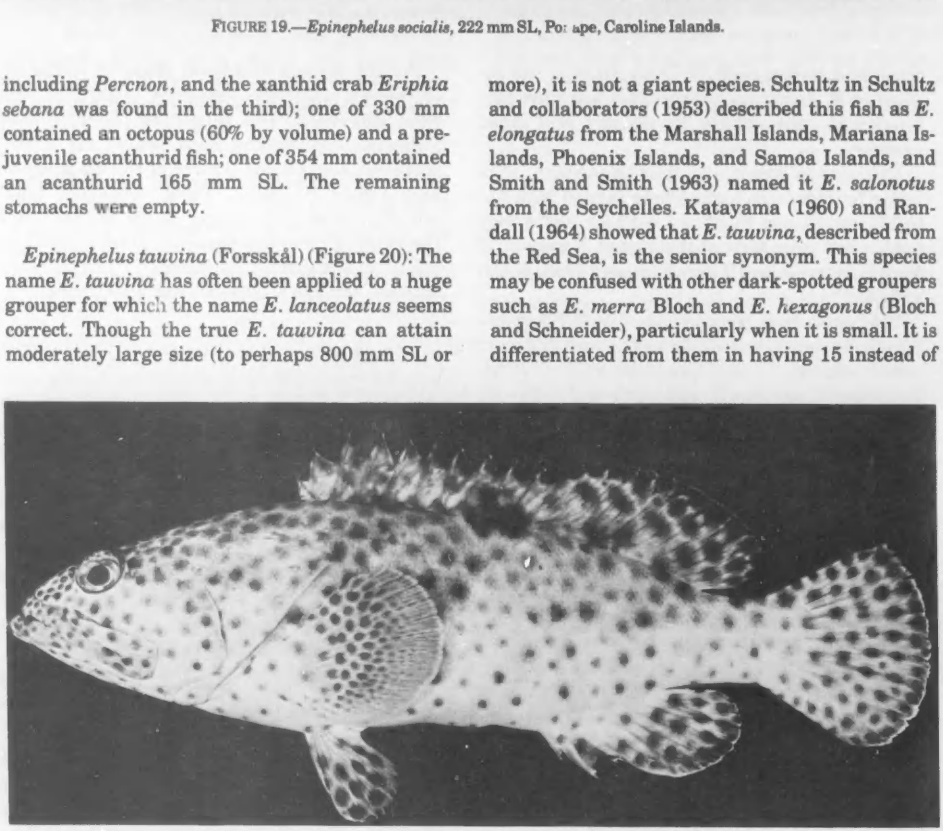

FIGURE 20.—*Epinephelus tauvina*, 252 mm SL, Enewetak, Marshall Islands.

16 soft rays in the dorsal fin, a total of 27-30 gill rakers, instead of 20-27, and a more elongate body.

Epinephelus tauvina is not very common in the Marshall Islands. It may be found in both lagoon and outer reef environments.

Six specimens from Enewetak, 324-434 mm SL, 0.45-2.54 kg, were tested. Four were nontoxic, and one each was poisonous at the 1 and 2 levels. One specimen from Bikini, 400 mm SL, was nontoxic, while a second, 450 mm SL (2.3 kg), gave a mongoose test of 3.

Randall and Brock (1960) found food in the stomachs of 3 of 12 specimens (identified as *E. elongatus*) collected in the Society Islands. All had eaten fishes; in addition, one stomach contained a crab chela.

Thirty-four specimens, 204-500 mm SL, from Enewetak, Society Islands, Line Islands, Cook Islands, Rapa, and the Red Sea were examined for food. Nineteen had empty stomachs, one contained a crab, and the rest had eaten fishes, of which one could be identified to species (*Adioryx lacteoguttatus*) and three to family (Pomacentridae, Holocentridae, and Mullidae).

Plectropomus leopardus (Lacepède) (Figure 21): This is the largest and most common of four groupers of the genus *Plectropomus* in the Marshall Islands. The genus is readily distinguished from other Micronesian serranid genera in having eight dorsal spines and large canine teeth in the jaws; also the body is more elongate than most other groupers. *Plectropomus leopardus* is reddish with small dark-edged blue spots and an emarginate caudal fin.

This species is among the worst offenders in Oceania for causing ciguatera. Halstead (1967) listed it as poisonous from Jaluit in the Marshall Islands and in the Tuamotus. He cited 10 papers that have reported on its toxicity in the Pacific, among them Randall (1958) who noted it as the most toxic of the groupers in Tahiti and reported his own poisoning from the Tuamotus.

Thirty-one specimens were collected at Enewetak for ciguatoxin content, mainly by spearing. The fish ranged from 426 to 790 mm SL and weighed from 1.8 to 11.8 kg. Twelve were nontoxic, six were poisonous at the 1 level, eight at 2, four at 3, and one (520 mm SL) was a 5. One specimen (8.2 kg) from Bikini was nontoxic.

Randall and Brock (1960) recorded the food of seven specimens from the Society Islands: four had empty stomachs and the rest had eaten fishes.

Thirty-seven specimens 426-790 mm SL were collected for food-habit study from Enewetak, Society Islands, and Okinawa. Fifteen had empty stomachs, and the rest contained fishes. Five had eaten parrotfishes (one grouper, 702 mm SL, contained a *Scarus gibbus* 313 mm SL). A 643 mm fish contained two acanthurids, one of which was a *Ctenochaetus striatus* 153 mm SL. A 705 mm grouper had eaten a labrid, *Cheilinus undulatus*, 270 mm SL. Two others had groupers in their stomachs, a 659 mm fish contained *E. tauvina* 267 mm SL, and a 790 mm fish contained a half-digested *Epinephelus* sp.

Plectropomus melanoleucus (Lacepède) (Figure 22): This distinctively colored grouper, white with

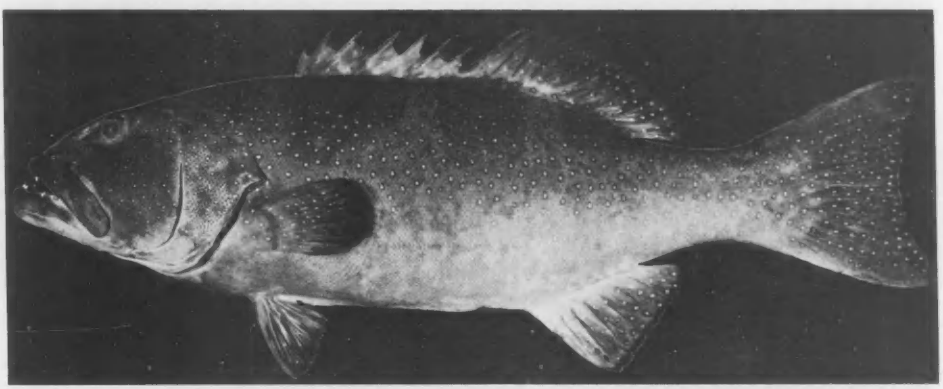

FIGURE 21.—*Plectropomus leopardus*, 513 mm SL, 3.4 kg, Enewetak, Marshall Islands.

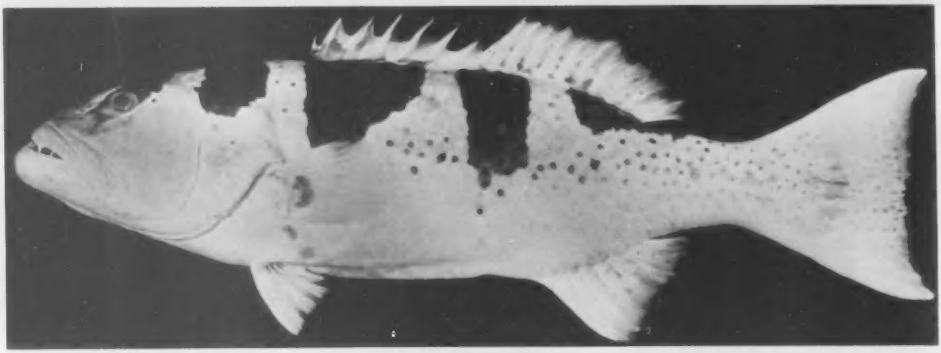

FIGURE 22.—*Plectropomus melanoleucus*, 492 mm SL, Enewetak, Marshall Islands.

black saddlelike bars, scattered small blue spots, and yellow fins has been regarded as a color phase of *P. maculatus* (Bloch) by a number of authors from Boulenger (1895) to Smith and Smith (1963). *Plectropomus melanoleucus*, however, is a valid species. In addition to color, it differs from *P. maculatus* (and *P. leopardus* and *truncatus*) by usually having 17 instead of 16 pectoral rays.

This species is rare in Oceania. Only a single specimen, 506 mm SL, 2.95 kg, was taken at Enewetak during the ciguatera survey. Its viscera produced a reaction of 2 when fed to a mongoose. Its stomach was empty.

Plectropomus truncatus Fowler (Figure 23): Like *P. leopardus*, this grouper has dark-edged blue spots, but the spots are larger in fishes of about the same size. The best field character to distinguish this species is its truncate caudal fin.

One specimen (384 mm SL, 1.45 kg) from Enewetak produced a ciguatoxic reaction of 2; its stomach was empty.

Hiatt and Strasburg (1960) reported one of three specimens of this grouper collected at Enewetak with a holocentrid fish in its stomach.

Variola louti (Forsskål) (Figure 24): This colorful grouper is yellowish brown to orange, profusely spotted with blue or pink (blue from shallow water, pink in deeper water), with broad zones of yellow posteriorly on the median and pectoral fins. Apart from color, it is readily distinguished by its deeply concave caudal fin. It is usually found on outer reefs at depths >15 or 20 m.

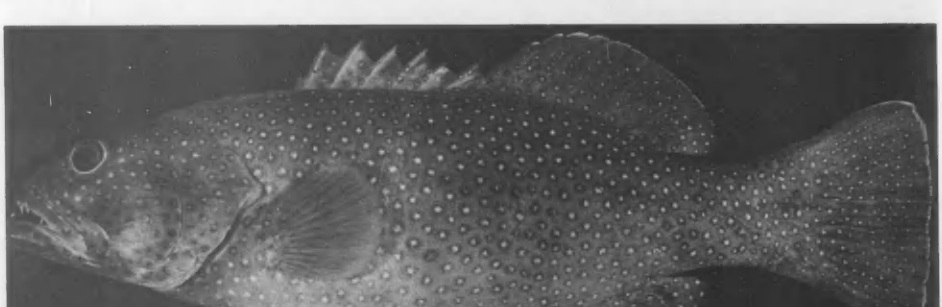

FIGURE 23.—*Plectropomus truncatus*, 350 mm SL, Enewetak, Marshall Islands.

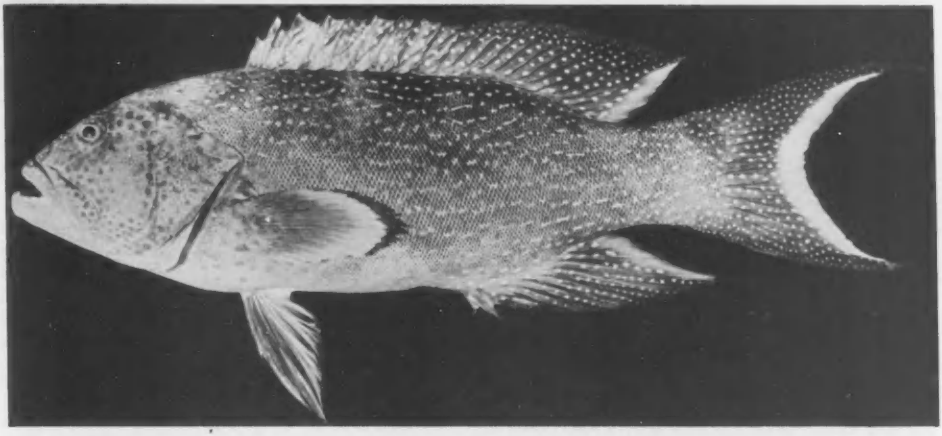

FIGURE 24.—*Variola louti*, 273 mm SL, Enewetak, Marshall Islands.

Variola louti is well known as a cause of ciguatera. In Mauritius it is prohibited from sale in fish markets. Toxicity there has been reported by Wheeler in Wheeler and Ommanney (1953).

Nineteen specimens were obtained for testing at Enewetak. They ranged from 352 to 418 mm SL and weighed from 1.1 to 2.2 kg. Thirteen were nontoxic, four gave a mongoose test of 1, and two a test of 3. Two from Bikini, 292 and 420 mm SL, were nontoxic.

Randall and Brock (1960) opened seven stomachs of the species from the Society Islands. Five were empty and two contained digested fishes. Hiatt and Strasburg (1960) found a juvenile unicornfish, *Naso* sp., in the stomach of one of two specimens from Bikini. Helfrich et al. (1968) examined the stomach contents of 44 specimens from the Line Islands. They found fishes, including acanthurids, balistids, and muraenids, in 80% of the stomachs, and crustaceans in 11%.

For the present food-habit study 44 specimens were examined. These ranged from 180 to 560 mm SL (largest weighed 5.45 kg). They were caught at Enewetak, Bikini, Line Islands, Tahiti, Rarotonga, Pitcairn Group, Rapa, and Tutuila. Twenty had empty stomachs. One contained a crab, one a spiny lobster, and the rest had eaten fishes, of which the following were identified at least to family: *Adioryx* sp. (120 mm specimen in a 295 mm grouper), *Scorpaena* sp. (28 mm specimen in a 235 mm grouper), *Parupeneus trifasciatus* (a 53 mm transforming specimen in a 470 mm grouper), juvenile *Chaetodon* sp., *Anampses caeruleopunctatus* (identified from scales), *Scarus sordidus* (140 mm specimen in a 375 mm grouper), and a pomacentrid.

Lutjanidae (Snappers)

Aprion virescens Valenciennes (Figure 25): This elongate snapper has been reported as poisonous from a number of Pacific localities, including the leeward Hawaiian Islands (Halstead 1967). Halstead did not list any Indian Ocean localities. It may therefore be worthy of note that the author incurred a mild case of ciguatera from eating a fish of this species at Mauritius. Also he was informed that poisoning is known from nearby Réunion.

Aprion virescens is a roving carnivore of open water but often found within or near reef areas, both in atoll lagoons and in outer reef zones. It is difficult to approach underwater; most of the specimens were obtained by hook and line, often while trolling.

Eleven specimens, 435-622 mm SL (1.6-5.2 kg), from Enewetak were tested. Eight were nontoxic, one (589 mm) gave a reaction of 1, one (622 mm) was a 3, and one (620 mm) a 4.

Eight were taken at Bikini ranging from 406 to 685 mm SL (1.8-5.4 kg). All, exept one of 457 mm SL which produced a mongoose reaction of 1, were nontoxic.

Ommanney in Wheeler and Ommanney (1953) reported on the analysis of stomach contents of 80 *A. virescens* from the Mauritius-Seychelles region. Forty-four of these were empty. The stomachs of

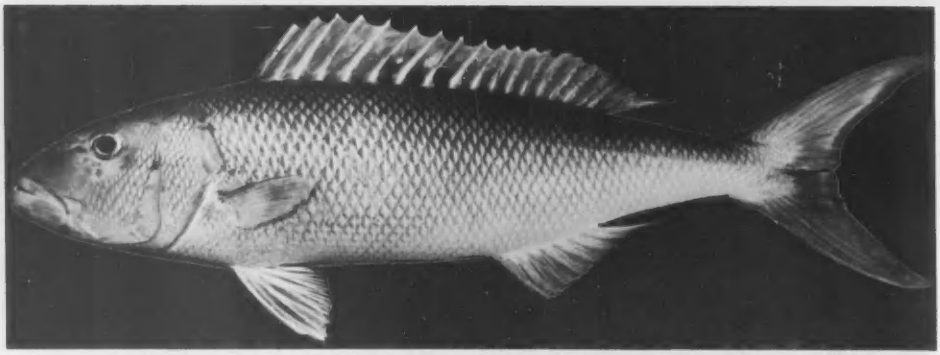

FIGURE 25.—*Aprion virescens*, 503 mm SL, 2.5 kg, Nuku Hiva, Marquesas Islands.

21 contained fishes; 6 had fishes and macroplankton; 5 had only macroplankton; and 4 contained cephalopods. Among the fishes taken from the stomachs were scarids, ostraciids, siganids, a bothid, and *Caesio coerulaureus*.

Talbot (1960) reported on 259 specimens caught by handline and surface lure on the east African coast which ranged from 202 to 800 mm SL (weight to 11.3 kg). He presented a diagram of the relative abundance of food organisms for this fish as follows: fishes 49%, plankton 17%, cephalopods 14%, and crustaceans exclusive of plankton (mainly portunid crabs) 12%. He did not indicate how many specimens had empty stomachs.

The stomachs of 15 specimens from the Marshall Islands and 1 from Hawaii were examined. Ten were empty. Four contained fishes; (one prey fish identified as *Scarus* sp.); one *A. virescens* (481 mm SL) had also eaten an octopus (one-third stomach volume). A 457 mm fish contained a 10 mm calappid crab, and one of 650 mm a stomatopod.

Lutjanus bohar (Forsskål) (Figure 26): This red snapper has been implicated more frequently in ciguatera than any fish of the Indo-Pacific region. It is probably the species which sickened the crew of Captain Cook in the New Hebrides in 1774 (Banner 1965). Its toxicity has also been reported under the junior synonym *Lutjanus coatesi* Whitley. This species occurs along seaward reefs and in passes. It is more common around atolls and low coral islands than high islands (Randall and Brock 1960). It is especially abundant in the Line Islands. Reef fishes became highly toxic there during and immediately after World War II; the toxicity declined in the early 1960's (Banner and Helfrich 1964). When the toxicity was high, *L. bohar* from these islands was used for the chemical and pharmacological work on ciguatoxin at the University of Hawaii (replaced by *Lycodontis javanicus* from Johnston Island in later years). It was the species used by Banner et al. (1966) to demonstrate the long periods of retention of ciguatoxin in the tissues of poisonous fishes when removed from the source of the toxin.

The toxicity of 95 specimens from Enewetak from 430 to 635 mm SL (2.5-7.5 kg) was tested. Fifty-six were nontoxic; 22 gave a mongoose test of 1; 11 were 2, 5 were 3, and 1 (533 mm) was a 5.

From Bikini 143 specimens which ranged from 330 to 760 mm SL were tested. Of these, 112 were nontoxic, 15 were 1, 8 were 2, 6 were 3, and 2 gave a mongoose test of 4.

From the atoll of Rongelap (lat. 11° N, long. 167° E) in the Marshall Islands we obtained 12 specimens of *L. bohar* which weighed from 3.2 to 9.1 kg. Eight of these were nontoxic, two gave a reaction of 2, one was a 3, and one a 5.

Hiatt and Strasburg (1960) found fragments of fish in one of two specimens of *L. bohar* from Bikini. Talbot (1960) examined 854 specimens from the East African coast; 58% had empty stomachs. Fishes composed 62% of the food material, crustaceans 24%, and mollusks 8%. Helfrich et al. (1968) determined the diet of 2,276 specimens from Palmyra and Christmas Islands in the Line Islands; 21.4% of these were empty. Fishes dominated the stomach contents (48.7% by volume at Palmyra and 65.4% at Christmas), of which acanthurids were the most common among those identified. Mollusks represented 19.1% by volume

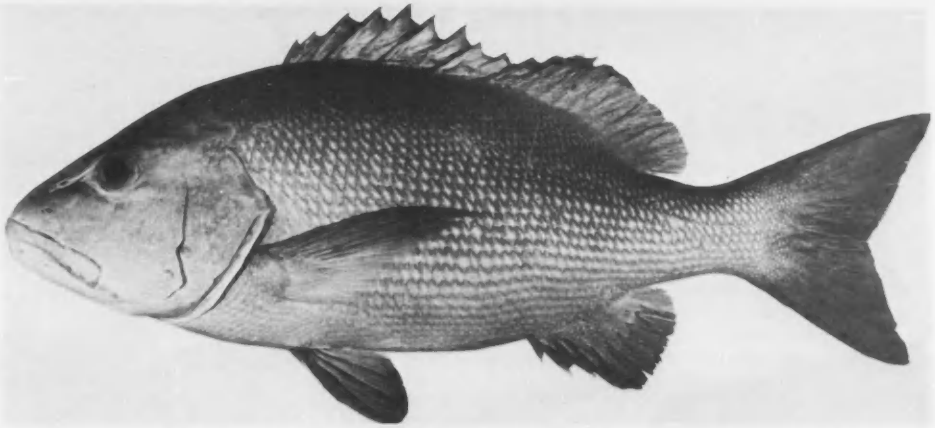

FIGURE 26.—*Lutjanus bohar*, 520 mm SL, 4.9 kg, Ulithi, Caroline Islands.

of the total food material at Palmyra and 18% at Christmas. Crustaceans (principally decapod megalops) composed 15.4% of the food among Palmyra fish and 13.3% of Christmas Island specimens.

The stomachs of 121 adult specimens of *L. bohar* from the Marshall Islands, 330-635 mm SL, most of which were taken by hook and line, were examined. Eighty-six were empty. Of those with identifiable food, 76.2% contained fishes (including *Lycodontis* sp., *Cephalopholis urodelus*, *Archamia* sp., *Lethrinus variegatus*, *Scarus* sp., and *Ostracion* sp.), 10.8% had eaten crabs (including portunids), 8.7% contained octopus, and 4.3% shrimps.

Lutjanus fulvus (Schneider) (Figure 27): The names *L. vaigiensis* (Quoy and Gaimard) and *L. marginatus* (Cuvier) are junior synonyms that have often been used for this snapper. It is yellowish on the body, the head gray, the caudal fin reddish black with a narrow white posterior border; the dorsal fin is reddish and the anal and pelvic fins yellow. It is a small inshore species, abundant throughout the Indo-West Pacific. It is found more often in sheltered than exposed environments. Hiyama (1943:48-49, pl. 6, fig. 17) reported that Marshallese natives informed him that this fish (which he identified as *L. flavipes* Valenciennes), rarely causes ciguatera; when it does, the cases are light. Halstead (1967:98, pl. 68, fig. 4) listed it among the ciguatoxic fishes [misidentified as *L. janthinuropterus* (Bleeker)].

Two specimens from Enewetak, 207 and 217 mm SL, were nontoxic.

Randall (1955a) examined the stomachs of six specimens taken with rotenone at Tarawa, Gilbert Islands. One had eaten a small holothurian, one a brachyuran crab, and two contained fishes that were probably prior victims of the ichthyocide. Hiatt and Strasburg (1960) analyzed the stomach contents of six juveniles from Arno, Marshall Islands; they reported the following food items: crabs, fishes, amphipods, shrimps, and stomatopods. Randall and Brock (1960) examined 50 specimens which had food in their stomachs; 54.3% of these contained crustaceans (mainly crabs) and 42.4% fishes. Helfrich et al. (1968) collected 51 specimens from Palmyra for food-habit study. The dominant food items were mugilid, mullid, and pomacentrid fishes; crustaceans made up the next most frequent organisms of the diet.

For the present study 44 specimens 182-250 mm SL were collected in the Marshall Islands, Mariana Islands, and Caroline Islands. Thirty-one of these had empty stomachs. Of those with food, 68.4% had eaten crustaceans (nearly all crabs, mainly calappids) and 31.6% fishes.

Lutjanus gibbus (Forsskål) (Figure 28): This snapper is also reddish like *L. bohar*, but it does not attain such large size. The dorsal profile of adults, beginning with the nape, is highly convex, which is the basis for the specific name. Schultz in Schultz and collaborators (1953) stated, "This species was taken only in moderately deep water.

FIGURE 27.—*Lutjanus fulvus*, 215 mm SL, Enewetak, Marshall Islands.

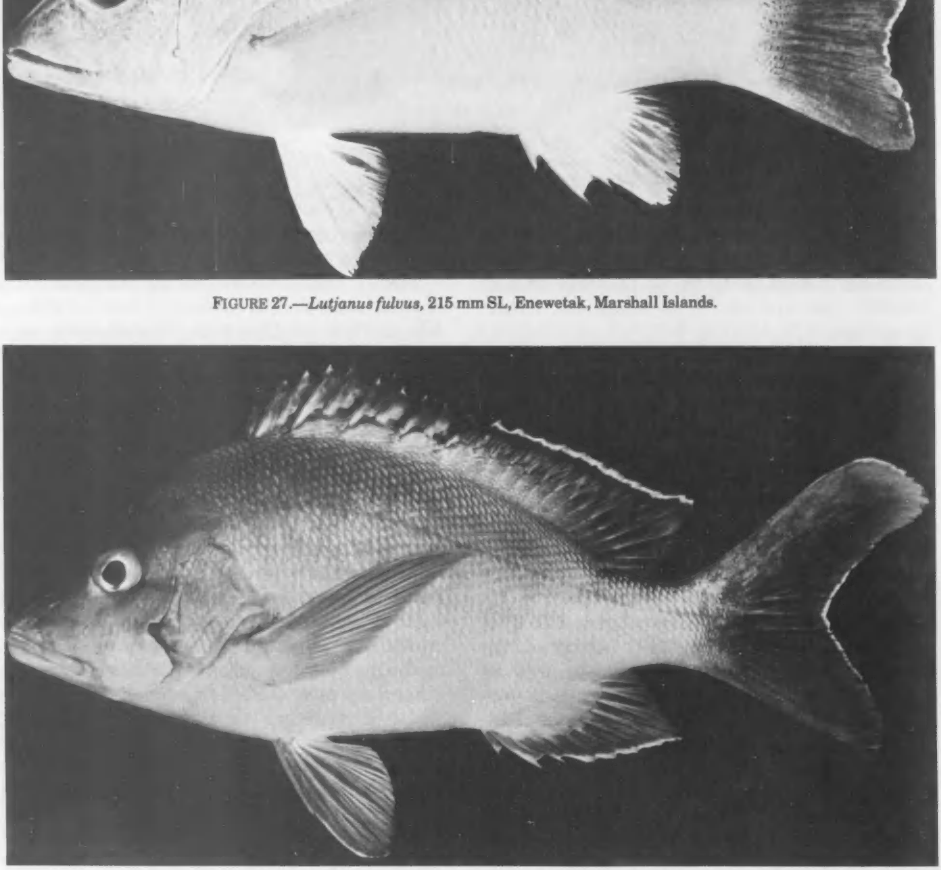

FIGURE 28.—*Lutjanus gibbus*, 291 mm SL, Palmyra, Line Islands.

It did not occur over the shallow parts of the reefs." Talbot (1960), on the other hand, wrote in reference to *L. gibbus* in east Africa, "It was only found in shallow water of from 3 to 8 fathoms." Actually, the species may occur either in the shallows or at moderate depths, but in the Marshall Islands, at

least, it is usually encountered in water of 20 m or more. Though mainly found on the outside of sea reefs and in passes, it may also occur in lagoons. It is often observed in large aggregations.

Thirty-one specimens of *L. gibbus* from Enewetak 302-375 mm SL (largest 1.8 kg) were collected. Twenty-one of these fishes were nonpoisonous; five were rated as 1, two were 2, and three ranked 3 by the mongoose test.

Thirty-five specimens from Bikini, 279-385 mm SL, were tested. All but three were nontoxic; the three toxic fish produced a mongoose reaction of only 1.

Randall and Brock (1960) collected 23 specimens in the Society Islands of which only 9 had food in their stomachs (5 of these were juveniles). The four adults contained fishes, crabs, and unidentified crustaceans. Hiatt and Strasburg (1960) examined 43 specimens (175-260 mm SL) from the Marshall Islands of which 10 had empty stomachs. Crustaceans were the main food, especially crabs (60% contained xanthids and 17% portunids); Amphineura were found in 13% of the stomachs. *Octopus*, *Natica*, *Ptychodera*, small holothurians, polychaetes, sipunculids, and fish *Apogon* were all found in 4% of the stomachs. Talbot (1960) reported on the capture of 121 specimens. He wrote, "Foods eaten were mainly crustaceans, including crabs and Penaeid prawns. Small coral fishes were also occasionally taken." Helfrich et al. (1968) found food in 36 of 45 stomachs of adults from the Line Islands; fishes were the main item of diet, with crustaceans the second most abundant. [Fishes included unidentified eels, acanthurids, and *Pomacentrus nigricans* (= *Stegastes nigricans*).] Most crustaceans were brachyuran crabs, but there were also alpheid shrimps and slipper lobster. Mollusk remains were mainly prosobranchs, but opisthobranchs and cephalopods were also found. Sea urchins were the most common of the miscellaneous invertebrates composing the rest of the stomach contents.

During the present study the stomachs of 51 specimens from the Marshall Islands, 260-419 mm SL, were examined. Twenty-seven were empty. Of those with food, 40% had eaten crabs, 26% fishes (including *Pseudocheilinus* sp. and *Adioryx microstomus*), 17% echinoids (including *Eucidaris* sp. and *Heterocentrotus mamillatus*), 12% ophiuroids (including *Ophiocoma erinaceus*), 2.1% alpheid shrimps, 2.1% octopus, and 0.3% gastropods.

Lutjanus monostigmus (Cuvier) (Figure 29): This species, named from the blackish spot usually present on its side (on lateral line), is capable of causing severe cases of ciguatera. Belotte (1955) gave the case history of an American who was in a coma 3 days after eating this snapper in Tahiti; the author also interviewed this man. The sale of this species in Tahiti, where it is called "taivaiva," (Randall 1972) is forbidden. It is found in reef environments from shallow water to moderate

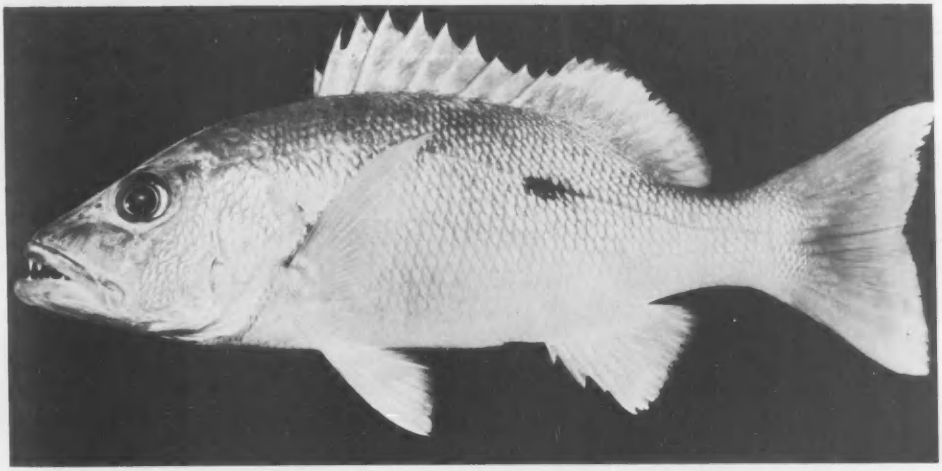

FIGURE 29.—*Lutjanus monostigmus*, 249 mm SL, Florida Island, Solomon Islands.

depths, especially where there is deep shelter. Not infrequently it is encountered in small aggregations. Adults are wary, hence difficult to spear.

Only three specimens were obtained from Enewetak, 310-420 mm SL (0.8-1.6 kg), for testing of toxicity. One was nontoxic, one was 1, and one a 2.

Five specimens, 400-445 mm SL, were collected in Bikini. Four were nontoxic; the largest gave a mongoose reaction of 1.

Randall and Brock (1960) opened 32 stomachs of adults of this species, of which 18 were empty. Those with full stomachs all contained fishes, among them *Decapterus pinnulatus*, *Selar crumenophthalmus*, and *Ctenochaetus striatus*. Hiatt and Strasburg (1960) found a goatfish in the stomach of one of three specimens from Enewetak; the other two were empty. Talbot (1960) collected 18 specimens off east Africa. He reported fish remains (including a mullid and a labrid) in most stomachs; penaeid prawn remains were also found. Helfrich et al. (1968) examined 29 specimens from the Line Islands. They found fishes in 92% of the stomachs and crustaceans (stomatopod larvae and one slipper lobster) in 23%.

For the present food-habit study 41 specimens of *L. monostigmus* were examined from the Marshall Islands, Society Islands, Line Islands, and Samoa Islands. Twenty-three had empty stomachs. Of those with food, 92% by volume had eaten fishes (including the holocentrid *Adioryx microstomus*, acanthurids, and a balistid), and 8% crabs (including a portunid).

Macolor niger (Forsskål) (Figure 30): Although not previously reported as poisonous, this lutjanid fish attains moderate size, is a reef-dweller, and carnivorous; this would seem to have the potential for causing ciguatera. A total of 25 adults, 403-445 mm SL (2.3-2.95 kg), were taken, all from Enewetak, and mainly from explosive stations in the lagoon. Twenty-three were nontoxic and two gave a reaction of 1 on the feeding of liver and viscera to mongooses.

The stomachs of eight adult specimens taken at 9:00 a.m. at Enewetak were examined. All were empty. The large eyes of this species is suggestive of nocturnal habits, and the numerous (about 72) long gill rakers would seem to indicate at least some feeding on zooplankton (perhaps more important in smaller individuals than large adults). Some of the specimens were caught by hook and line baited with fish. Hiatt and Strasburg (1960) also reported that this species can be caught on a baited hook.

Lethrinidae (Emperors)

Lethrinus amboinensis Bleeker (Figure 31): Following Sato (1978), this emperor is identified as *L. amboinensis*. It lacks characteristic color markings, being light brownish to greenish dorsally

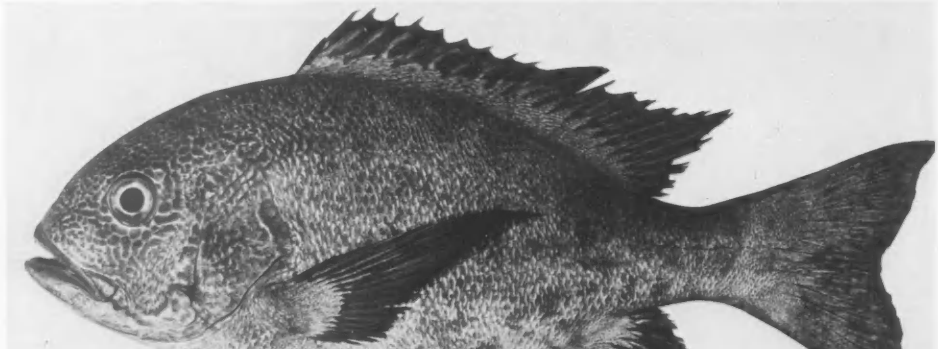

FIGURE 30.—*Macolor niger*, 378 mm SL, Enewetak, Marshall Islands.

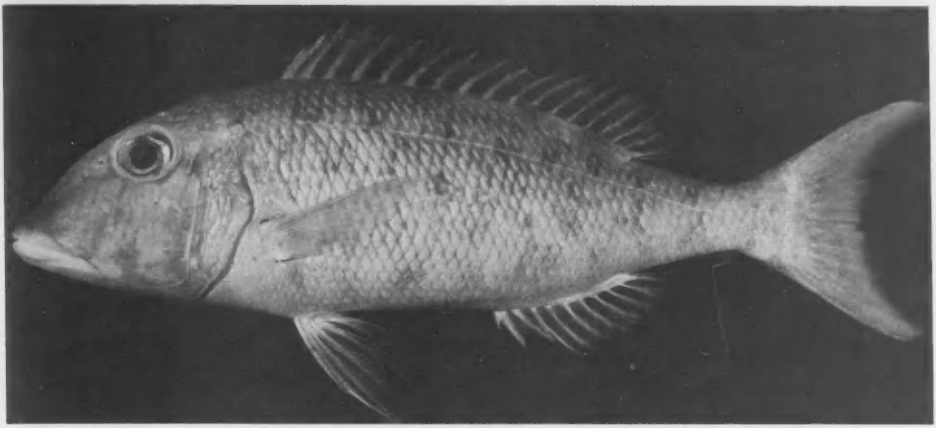

FIGURE 31.—*Lethrinus amboinensis*, 294 mm SL, Enewetak, Marshall Islands.

with small dark brown spots and blotches, shading to white ventrally. It is somewhat elongate, the head length greater than the depth; the snout is moderate, its length in adults 1.8-1.0 in head length; the maxilla reaches a vertical a little posterior to the anterior nostril. The teeth along the sides of the jaws are conical.

Twenty-four specimens were taken at Enewetak and nine at Bikini, the largest 310 mm SL. All were nontoxic.

Helfrich et al. (1968) determined the food of 14 specimens of *L. amboinensis* from Palmyra, Line Islands. Fishes were found in 75% of the stomachs, mollusks in 25%, and crustaceans in 17%; all specimens had some sea urchin fragments.

Fish remains were found in one of two stomachs examined at Bikini.

Lethrinus kallopterus Bleeker (Figure 32): This *Lethrinus* is distinctive in having orange fins and blackish spots over occasional scales; the snout is short, the maxilla reaching a vertical at anterior edge of eye. The teeth at the sides of the jaws are nodular (i.e., neither conical nor well-developed molars). It was most often seen in the deeper parts of the atoll lagoons.

A total of 19 specimens were collected at Enewetak for the testing of toxicity. These ranged from 337 to 443 mm SL (1.1-2.7 kg). Fourteen were nontoxic, two produced a reaction of 1, two were 2, and one (368 mm SL) was a 5.

Two specimens, 330 and 457 mm SL, were procured from Bikini; neither was toxic.

The stomachs and intestines of 13 specimens, 330-443 mm SL, from the Marshall Islands were opened. Five of the fish were empty. Four had eaten only echinoids (including *Echinometra mathaei*); one contained mostly echinoids but also the cowrie *Cypraea carneola*; another (the largest) had eaten just the cowrie *C. vitella*; still another had a cowrie in its gut (20% by volume of the food material), and the rest of the food material consisted of crinoids; one specimen contained only a starfish arm.

Lethrinus miniatus (Forster in Bloch and Schneider) (Figure 33): This emperor has an especially long snout (1.6-1.8 in head length of adults). It is primarily gray in color, but can alter its pattern, like many other *Lethrinus*, to one of dark irregular bars and blotches. Often there are two or three bluish streaks on the snout passing anteriorly and diagonally downward from the eye. The teeth on the sides of the jaws are conical. This species was seen in both lagoon and outer reef environments, but mainly in lagoons. It is among the largest of the emperors, reported to attain 1 m.

Of nine adults, 435-530 mm SL (1.8-3.6 kg), which were caught at Enewetak, six were nontoxic, and three gave a reaction of 3.

Twelve specimens from Bikini, 381-635 mm SL, 1.4-7.3 kg, were nontoxic.

Eight of 14 specimens from Enewetak and Bikini had food in their stomachs. Three contained fish remains, one of which (456 mm SL) included a

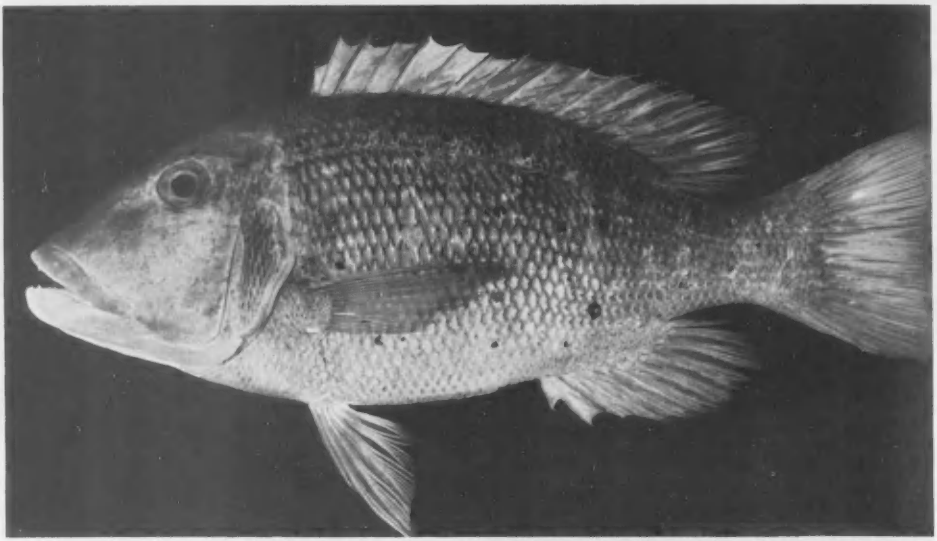

FIGURE 32.—*Lethrinus kallopterus*, 345 mm SL, Enewetak, Marshall Islands.

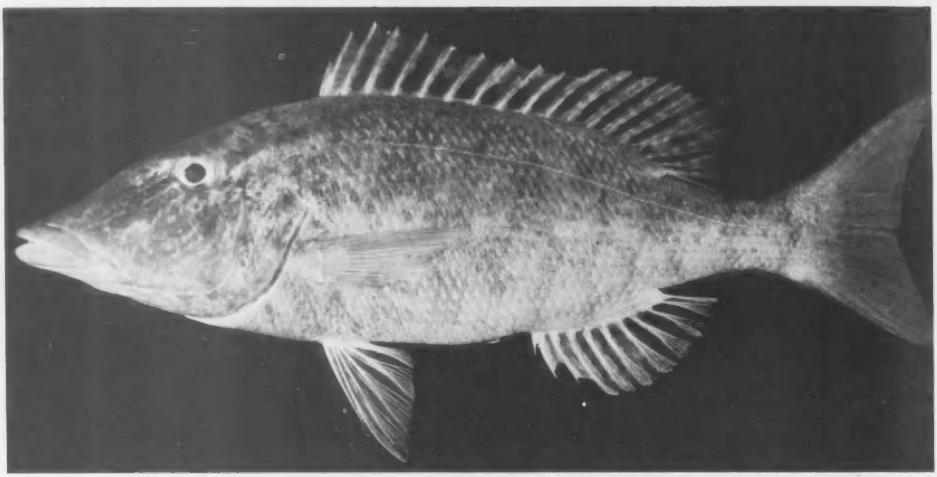

FIGURE 33.—*Lethrinus miniatus*, 430 mm SL, Enewetak, Marshall Islands.

Lethrinus 115 mm SL; the remaining three had eaten crustaceans (stomatopod, crab, and alpheid shrimp).

Lethrinus xanthochilus Klunzinger (Figure 34): This emperor is one of the more slender species of *Lethrinus* (depth 3.1-3.3 in SL). The interorbital space is nearly flat. The teeth on the sides of the jaws are conical. The upper lip is orange-yellow, and there is a red spot at the upper pectoral base. It is found more in lagoons than exposed reef habitats; it will venture into shallow water.

Two specimens, 445 and 550 mm SL (smallest 1.7 kg, largest not weighed), were collected at

FIGURE 34.—*Lethrinus xanthochilus*, 395 mm SL, Fanning Island, Line Islands.

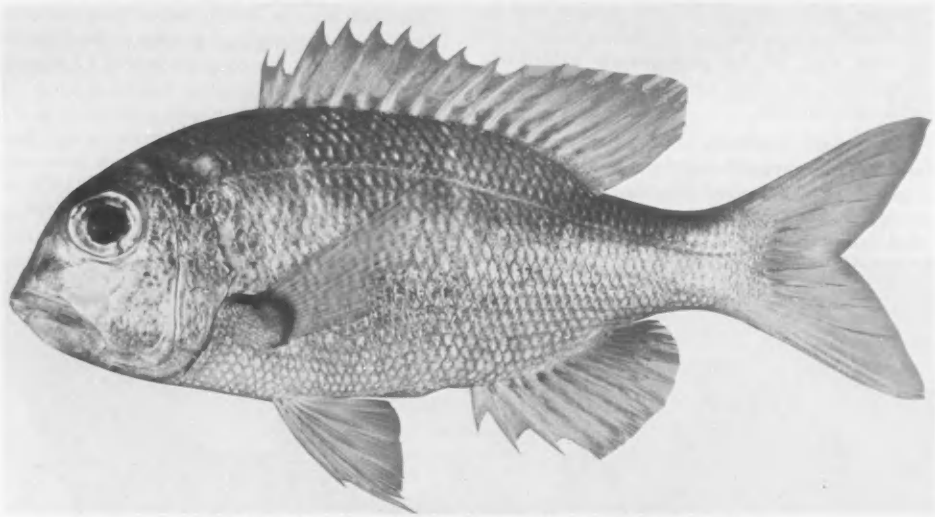

FIGURE 35.—*Monotaxis grandoculis*, 220 mm SL, Enewetak, Marshall Islands.

Enewetak; two, 305 and 432 mm SL, were taken at Bikini. All were nontoxic.

The stomach and gut contents of these four specimens and one of 466 mm from the Society Islands were examined. One fish contained crushed echinoids, one the remains of a calappid crab, one a digested fish, another both crab and fish remains, and one (the largest) a freshly ingested fish (probably from a rotenone station).

Monotaxis grandoculis (Forsskål) (Figure 35): *M. grandoculis* has been classified in the past principally in the Sparidae or Lutjanidae, but is now recognized as a lethrinid. It is readily distinguished by its large eyes, short blunt snout, and single row of well-developed molariform teeth along the side of the jaws. It occurs in a wide variety of reef habitats. Adults are difficult to approach underwater. This fish feeds mainly on in-

vertebrates with calcareous or chitinous hard parts. Although rarely implicated in serious cases of poisoning, it is capable of being ciguatoxic. Halstead (1967) listed 11 references attesting to its toxicity.

Five specimens, 277-362 mm SL (0.73-1.6 kg), from Enewetak were tested for toxicity. Four were nontoxic and one gave a reaction of 1 from the mongoose feeding.

Randall (1955a) reported on the gut contents of two specimens, 158 and 160 mm SL, from the Gilbert Islands; these consisted mainly of crushed shells of small mollusks and sea urchins. Hiatt and Strasburg (1960) examined the contents of the digestive tracts of eight specimens, 195-220 mm SL, from the Marshall Islands. One fish was empty. Crushed gastropods (including *Atys* sp. and *Cerithium* sp.) were found in all stomachs, pelecypods in 71%, crabs in 42%, hermit crabs in 28%, and spatangids and polychaetes each in 14%. Hobson (1974) collected five specimens in Hawaii. He found the principal prey, in order of importance in the diet, to be prosobranch gastropods, ophiuroids, echinoids, opisthobranch gastropods, and pagurid crabs.

Forty-eight specimens of *M. grandoculis*, 155-440 mm SL, were collected from the Marshall Islands, Line Islands, Cook Islands, Society Islands, Pitcairn, Hawaiian Islands, New Guinea, and the Red Sea for the study of food habits. Unless fish of this species are captured during the night or very early morning hours, their stomachs are nearly always empty. Occasional feeding by *M. grandoculis* does occur during the day, as indicated by Hiatt and Strasburg's (1960) observation of its "blowing" away sand to expose fossorial forms. Also one specimen taken at 2 p.m. during the author's survey had the remains of a freshly ingested crab in its stomach. Five of the fish collected in late afternoon hours had completely empty digestive tracts. The remaining fishes contained, on a volume basis, 39.4% gastropods, 18.9% crabs, 16.8% pelecypods, 13.9% echinoids (principally *Echinometra* and spatangoids such as *Clypeaster*), 6.1% pagurid crabs, 1.7% ophiuroids, 1.2% polychaetes, 1.0% unidentified worms, 0.7% fishes, and 0.3% foraminifera.

Kyphosidae (Sea Chubs)

Kyphosus cinerascens (Forsskål) (Figure 36): This chub may be distinguished from the other *Kyphosus* by the high soft portion of the dorsal fin (longest dorsal spine contained about 1.8 times in longest soft ray). It occurs in lagoon or outer reef areas and is often seen in loose aggregations. It is associated with hard substratum for its algal food, generally in the vicinity of crevices or caves with more than one entrance. Bartsch et al. (1959) reported this species as toxic from Majuro, Marshall Islands, but their data and the few other records of

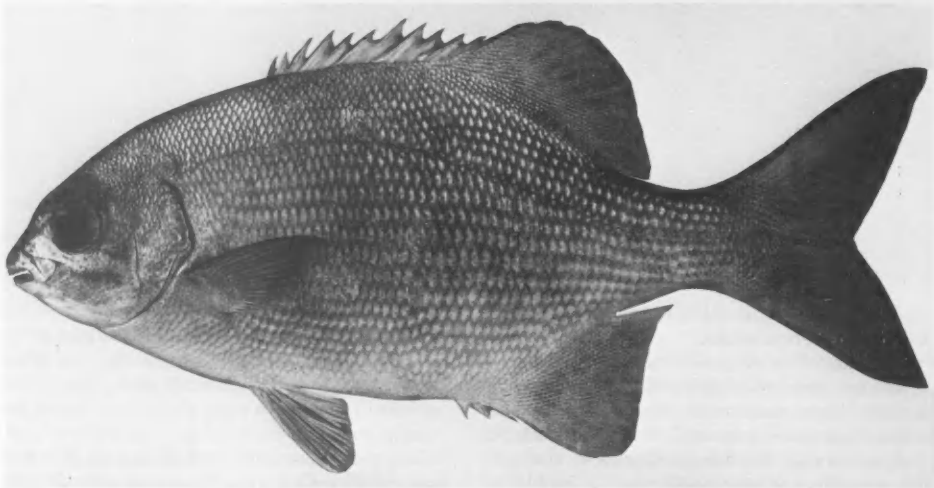

FIGURE 36.—*Kyphosus cinerascens*, 234 mm SL, Enewetak, Marshall Islands.

toxicity would seem to indicate that it is only marginally a cause of ciguatera.

Of two specimens from Enewetak, 356 and 364 mm SL, 1.8 kg, one was nonpoisonous and the other toxic at level 1.

Hiatt and Strasburg (1960) found benthic algae in the stomachs of three of four specimens examined in the Marshall Islands. Hobson (1974) reported algae in three stomachs from Hawaii; however, *K. cinerascens* apparently does not occur in the Hawaiian Islands (though two other species are present).

Three specimens, 330-364 mm SL, from Enewetak were opened. The stomach of one was empty, and the other two contained benthic algae. The algae of one were identified by Tsuda[8] as the reds *Gelidium pusillum*, *Champia parvula*, and *Leveillea jungermannoids* (90%) and the brown *Sphacelaria tribuloides*.

Carangidae (Jacks)

Caranx ignobilis (Forsskål) (Figure 37): This steep-headed jack is the largest species of the genus. Bagnis et al. (1972) stated that it can attain a length of 2 m and a weight of 80 kg. It can be differentiated from other Marshall Islands species by the absence of scales on the thorax except for a small median patch. Like other large carangids, it is a roving carnivore; it may be encountered anywhere in the atoll environment including water surprisingly shallow for such a large fish.

The author interviewed a man and wife in Moorea who were poisoned from eating the liver of a large individual of this species (estimated 1.5 m) which overturned their canoe in the long struggle to catch it. Both were very ill with ciguatera, the man comatose for several hours.

Five specimens, 573-920 mm FL, 3.6-16.3 kg, were obtained at Enewetak for the testing of toxicity. Three gave a 0 reaction and two a reaction of 1. Two specimens from Bikini, 635 and 1,105 mm FL, 4.5 and 27.3 kg, were nontoxic.

A total of 14 specimens were collected for food-habit study from the Marshall Islands, Line Islands, Hawaiian Islands, Pitcairn Group, and the Marquesas. Seven stomachs were empty, and the rest contained the digested remains of fishes, of which only one could be identified to species, the surgeonfish *Zebrasoma flavescens*. One stomach-content fish was a scorpaenid, and another (from a jack of 1,217 mm FL, 37.5 kg) a scarid.

Caranx lugubris Poey (Figure 38): The black jack is a circumtropical species with a well-earned reputation for causing ciguatera. Although the

[8]Roy T. Tsuda, Marine Laboratory, University of Guam, Box EK, Agaña, Guam 96910, pers. commun. 1972.

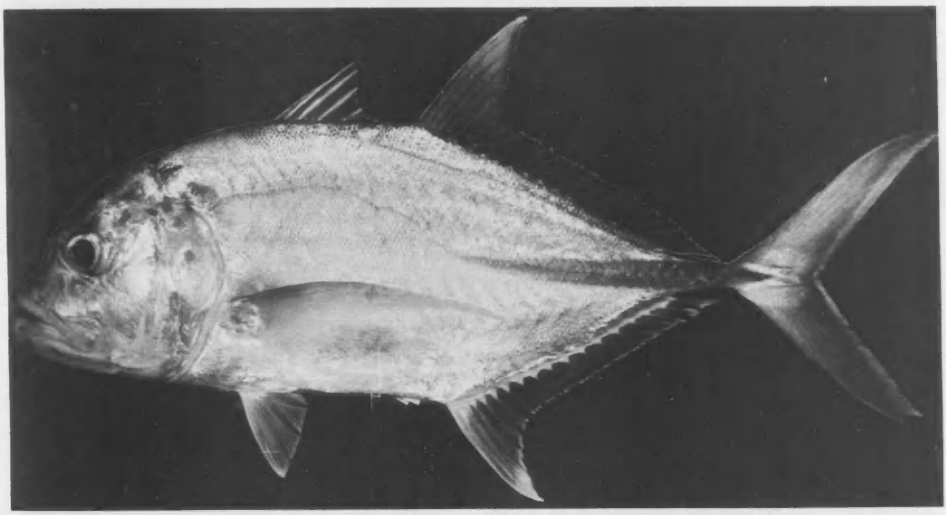

FIGURE 37.—*Caranx ignobilis*, 378 mm FL, Fanning Island, Line Islands.

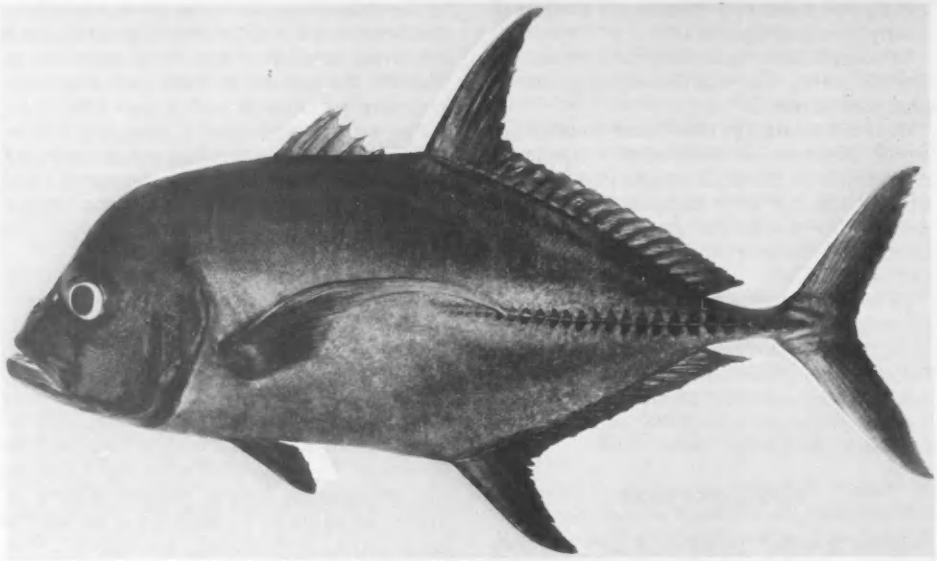

FIGURE 38.—*Caranx lugubris*, 557 mm FL, 3.1 kg, St. John, U.S. Virgin Islands.

dark color (especially on the scutes) and distinctive configuration generally permit identification, the fully scaled breast will provide separation from *C. ignobilis*, the low number of scutes on straight portion of lateral line (26-33) from *C. melampygus*, and the high gill raker count (18-20 on lower limb) from *C. sexfasciatus*. This species is found mainly around oceanic islands and is nearly always encountered in the clear water of outer reef environments.

Fifteen specimens were obtained at Enewetak for testing. These ranged from 488 to 910 mm FL and weighed from 2.5 to 15.5 kg. Eleven were nonpoisonous, two gave reactions of 1, one was a 2, and one a 3. No specimens were collected at Bikini.

Randall (1955a) reported a fish in one of two specimens collected in the Gilbert Islands and Randall (1967) found fishes in two of six specimens from the Caribbean Sea.

For the present food-habit study, 10 specimens were obtained from Enewetak and Henderson Island in the Pitcairn Group. Four had empty stomachs, and the remaining six contained the remains of fishes, one of which was a labrid.

Caranx melampygus Cuvier and Valenciennes (Figure 39): This is the most abundant jack of the genus in Oceania; it is widespread in the tropical and subtropical Indo-West Pacific and ranges to the eastern Pacific as well. It is irridescent blue along the back and median fins in life with a scattering of small blackish spots on the head and body except ventrally. The chest is completely scaled, and there are 38-44 scutes in the straight portion of the lateral line.

Thirty specimens were collected at Enewetak, 417-722 mm FL, 1.4-6.8 kg, for the assay of ciguatera. Twenty-four were nontoxic, four gave a reaction of 1, one was a 2, and one a 3.

Six specimens from Bikini, 394-686 mm FL, 1.8-6.6 kg, were nontoxic.

Randall (1955a) examined the stomach contents of four specimens from the Gilbert Islands. Two contained many small freshly ingested fishes which were probably the result of a rotenone station kill. Of the other two which were speared, one contained the anthiine fish *Mirolabrichthys tuka* (= *Anthias pascalus*). Hiatt and Strasburg (1960) found fish in the stomachs of two from the Marshall Islands, one of which was identified as *Trachurops* (= *Selar*) *crumenophthalmus*. Hobson (1974) examined the stomach contents of six specimens from Hawaii. One contained larval fishes and mysids, a second had fish and shrimp remains, and three contained well-digested fragments at least one of which was fish.

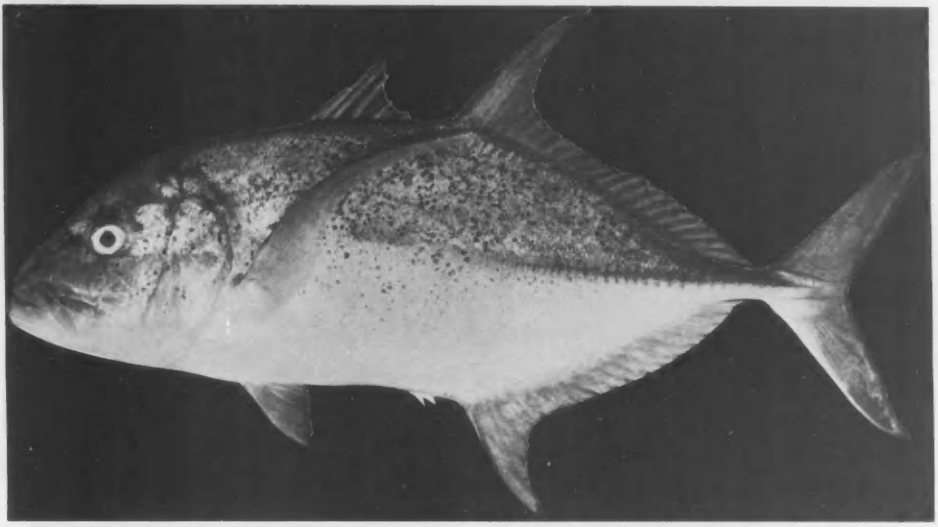

FIGURE 39.—*Caranx melampygus*, 498 mm FL, 1.9 kg, Sanganeb Atoll, Red Sea.

Sixty-one specimens, 298-722 mm FL, from the Marshall Islands, Hawaiian Islands, Line Islands, Marcus Island, Solomon Islands, and the Red Sea were collected for stomach-content study. Seventeen stomachs were empty. All the others contained the digested remains of fishes, though one had, in addition, a squid pen. The following fishes were identified from the stomach material: eel, *Anthias thompsoni*, *Caranx* sp. (90 mm FL in a 520 mm *C. melampygus*), *Priacanthus cruentatus*, *Cirrhitops fasciatus*, *Caesio* sp., *Parupeneus* sp., *P. trifasciatus*, *Pomacentrus pavo*, *Chromis caerulea*, labrid, *Thalassoma purpureum*, *Ptereleotris microlepis*, *Caracanthus unipinnus*, *Acanthurus triostegus*, acronurus stage of acanthurids (in two stomachs), and a subadult acanthurid.

Caranx sexfasciatus Quoy and Gaimard (Figure 40): This jack, which ranges from the Red Sea to eastern Oceania, is closely related to *C. hippos* of the Atlantic. It is usually seen in small schools, but is not common in the Marshall Islands. It is more elongate than the *Caranx* spp. discussed above, and it has a larger eye. The lower-limb gill raker count is 15-17. The scutes are blackish, there is a small black spot at the upper end of the gill opening, and the soft dorsal and anal fins are tipped with white. The dark bars of the young are the basis for the specific name.

Only two specimens were caught at Enewetak, 496 and 700 mm FL, 2.3 and 4.6 kg. Both were nontoxic. No specimens were obtained from Bikini.

Ommanney in Wheeler and Ommanney (1953) reported on the stomach contents of specimens caught during a survey of the Mauritius-Seychelles region. Eight specimens contained fish remains, one had squid remains, one had megalops larvae, and nine were empty. A parrotfish and two eels were noted among the stomach contents.

The stomachs of six specimens of *C. sexfasciatus*, 385-700 mm FL, from Enewetak and Tahiti were opened. Five were empty, and one contained well-digested fish remains. (This jack was speared at 11:30 a.m.)

Bagnis et al. (1972) stated that *C. sexfasciatus* is nocturnal. Wheeler and Ommanney (1953) on the other hand, wrote, "It often takes a lure..."; presumably he meant one trolled by day.

Scombridae (Tunas)

Gymnosarda unicolor (Rüppell) (Figure 41): The dogtooth tuna is named for its large conical teeth; it is also unique in having two patches of villiform teeth on the tongue. It lacks dark stripes or spots on the body; the second dorsal and anal fins are

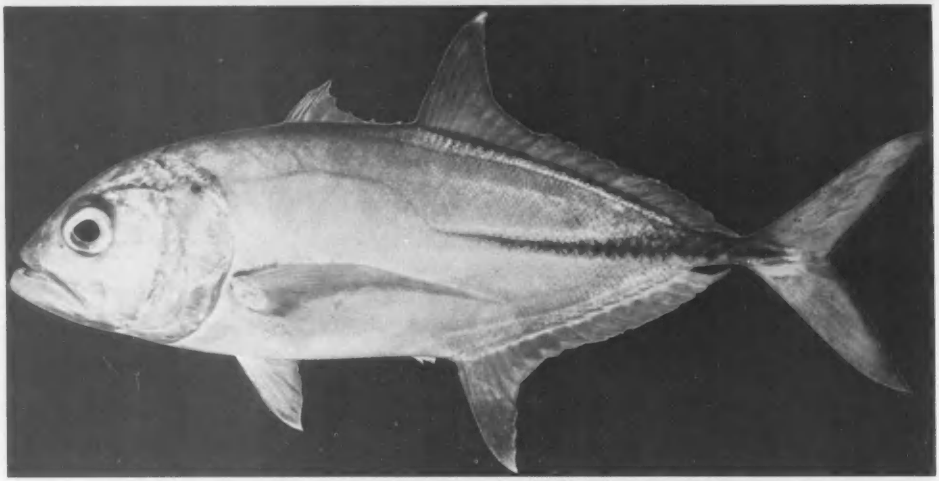

FIGURE 40.—*Caranx sexfasciatus*, 472 mm FL, 1.8 kg, Enewetak, Marshall Islands.

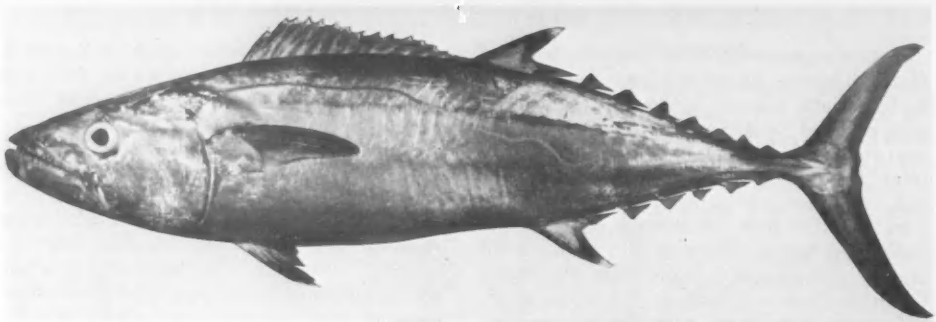

FIGURE 41.—*Gymnosarda unicolor*, 645 mm FL, 3.6 kg, Enewetak, Marshall Islands.

white tipped. A large species, Masuda et al. (1975) recorded it to a length of 2.4 m. Unlike other large tunas, in general, it occurs in relatively shallow coastal water, often around coral reefs, and it readily penetrates the deeper lagoons of atolls.

Thirteen individuals were collected from Enewetak which ranged from 550 to 1,350 mm FL (3.2-35.4 kg). Seven caused no symptoms when liver tissue was fed to mongooses; four produced a reaction of 1, one was a 2, and one a 3.

Three from Bikini, 737-940 mm FL, 6.4-11.8 kg, were nontoxic.

Hiatt and Brock (1948, after unpublished data of J. Marr and O. Smith) stated that the scad, *Decapterus sanctaehelenae*, was most frequently encountered in the stomachs of dogtooth tunas in the Marshall Islands. Schultz in Schultz and collaborators (1953) reported that *D. muroadsi* and *Caesio xanthonotus* were regurgitated by *Gymnosarda nuda* (= *G. unicolor*) which were caught at Bikini.

Five of 17 specimens from the Marshall Islands taken during the survey had empty stomachs. The others contained fishes, five of which were identified as: *Naso brevirostris*, *N. vlamingii*, *Cirrhilabrus* sp., *Caesio* sp., *Pterocaesio* sp. The two prey specimens of *Naso* were large adults. The *N. vlamingii*, taken from the largest *G. unicolor*, measured 370 mm SL.

Labridae (Wrasses)

Cheilinus undulatus Rüppell (Figure 42): The giant humphead wrasse is one of the largest of bony fishes. It has been recorded to a length of 2.29 m and a weight of 190.5 kg (Marshall 1964). The hump on the forehead develops only on larger individuals. Two dark lines which extend posteriorly from the eye are useful in identifying juveniles and subadults of this species. It is usually found on outer reef slopes or in deep channels, but also occurs in lagoons. It is difficult to approach underwater. According to Bagnis et al. (1972) individual fish have a home cave to which they retreat when threatened and to which they retire at night. Randall (1958) reported this species as capable of being moderately to strongly toxic in Tahiti, where it is called "mara" (Randall 1972). It is one of nine species of fishes which are banned from sale in the Papeete market (Bagnis 1968).

Seven specimens, 515-995 mm SL, the largest weighing 34.5 kg, were procured at Enewetak for testing. The largest gave a reaction of 2 on feeding to mongooses; the others were 0.

Randall et al. (1978) reported on the food habits of the giant humphead wrasse based on the examination of 72 specimens from the Red Sea and islands of Oceania. The diet is highly varied, the dominant groups of food organisms being mollusks (gastropods a little more numerous than pelecypods), crustaceans (especially crabs), echinoids, and fishes. The hard parts of the invertebrates are crushed to fragments by the powerful pharyngeal dentition.

Coris aygula Lacepède (Figure 43): This is one of the two largest species of *Coris* (the other an undescribed endemic from Lord Howe Island). The largest collected, from the Red Sea, measured 465 mm SL and 583 mm TL. Adult males develop a gibbosity on the forehead similar to that of *Cheilinus undulatus*, but these two wrasses could hardly be confused; the *Coris* is more elongate (depth about 3.2 in SL) and has small scales (60-65 lateral line scales for *C. aygula*, compared with about 25 for *Cheilinus undulatus*); also, the lateral line of *Cheilinus* is interrupted.

Coris aygula has apparently not been reported as causing ciguatera but because of its large size and similar food habits it would seem to be at least as suspect as *C. gaimard* which is known to be poisonous at times. The latter is more colorful, displaying bright blue spots and a yellow caudal fin.

Five adults of *C. aygula*, 329-377 mm SL (0.9-1.9 kg), were obtained from Enewetak for testing. One of 368 mm SL (1.4 kg) produced a toxic reaction of 1 when its liver and viscera were fed to a mongoose; the others were nontoxic.

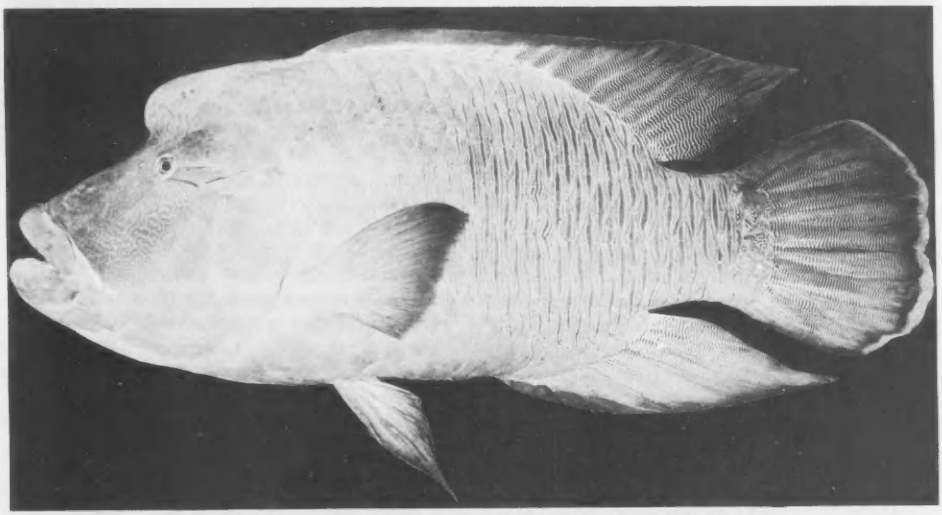

FIGURE 42.—*Cheilinus undulatus*, 915 mm SL, 25.8 kg, Enewetak, Marshall Islands.

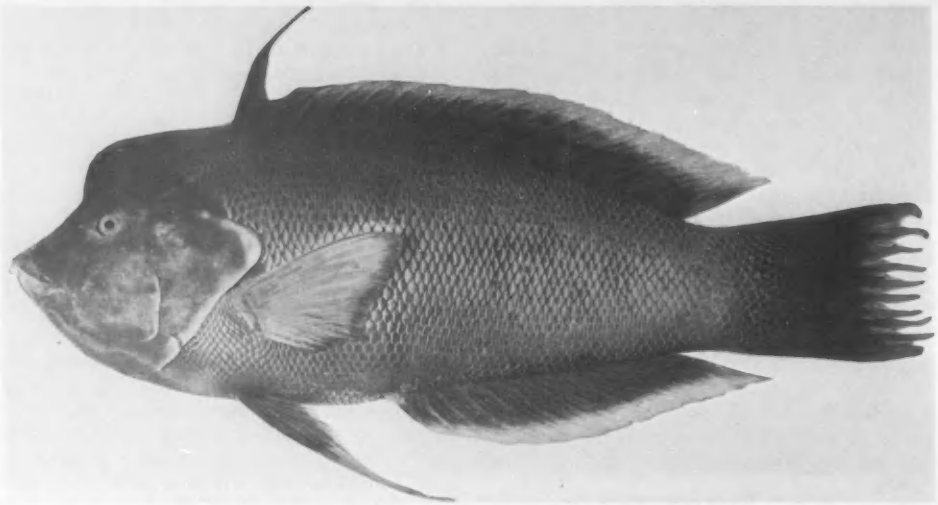

FIGURE 43.—*Coris aygula*, 380 mm SL, Marcus Island.

Al-Hussaini (1947) listed the food of the species as gastropods (*Turbo, Trochus*), *Dentalium*, and hermit crabs. Hiatt and Strasburg (1960) found the crushed remains of sand-dwelling pelecypods and gastropods in a single specimen (identified as *C. angulata*) from Enewetak.

Randall, G. J. Vermeij, and H. A. Rehder (manuscript in progress) will report in detail on the food habits of this wrasse. The principal food animals are gastropods, pelecypods, pagurid crabs, echinoids, and brachyuran crabs.

Epibulus insidiator (Pallas) (Figure 44): This unmistakable labrid, popularly known as the slingjaw wrasse because of its ability to enormously protrude its mouth, occurs from the Red Sea and east Africa to French Polynesia. Halstead (1967) listed nine references citing it as ciguatoxic.

Five specimens from Enewetak, 175-228 mm SL, 0.34-0.55 kg, were tested for toxicity. None caused any symptoms in the mongooses.

Hiatt and Strasburg (1960) collected one specimen from Enewetak and one from Bikini for food-habit study; both fish had eaten alpheid shrimps. They wrote, "This wrasse habitually feeds in ramose corals by extending its exceedingly protractile snout into the interstices to capture small alpheid shrimps and xanthid crabs living there."

For the present food-habit study 16 specimens, 183-240 mm SL, were collected from the Marshall Islands, Johnston Island, American Samoa, and the Society Islands. Two had empty stomachs; six had eaten only fishes and four only crabs. Other food items were shrimps, unidentified crustaceans, polychaetes, bryozoans, and unidentified eggs.

Scaridae (Parrotfishes)

Hipposcarus harid (Forsskål) (Figure 45): Smith (1956) created a new genus, *Hipposcarus*, for this species on the basis of the triangular patch of scales on the cheek with three or four rows behind, pointed snout, and minute nostrils. Although Schultz (1958, 1969) did not recognize this genus, it will be considered valid by Nelson and Randall.[9]

Smith (1959) described a Philippine form of this species as new, naming it *H. schultzi*. Schultz (1969) preferred to regard this form, for which he gave the range central and western Pacific Ocean, as a subspecies, *Hipposcarus harid longiceps* (Cuvier and Valenciennes).

Halstead (1967) has listed four references reporting the occasional toxicity of this parrotfish.

[9]G. J. Nelson, Department of Ichthyology, American Museum of Natural History, New York, and the author conferred in October 1977 on the generic limits of the Scaridae. Eventual publication is planned.

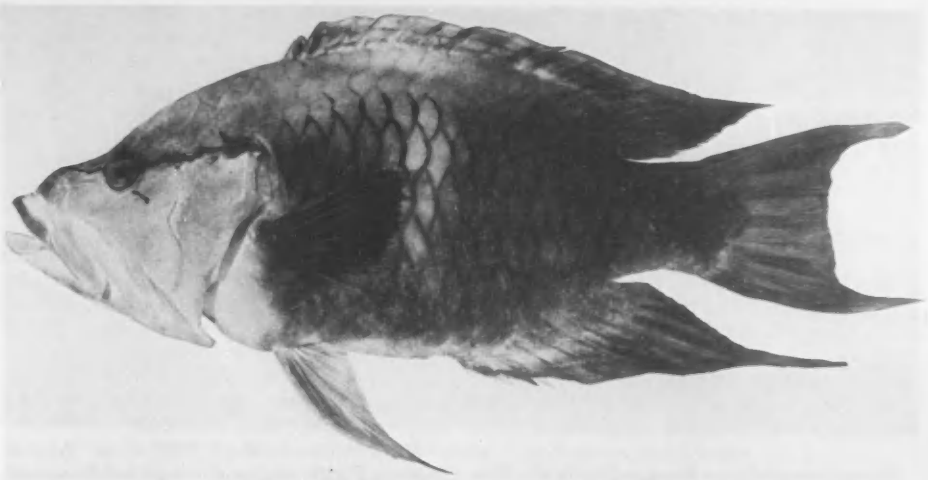

FIGURE 44.—*Epibulus insidiator,* 185 mm SL, Enewetak, Marshall Islands.

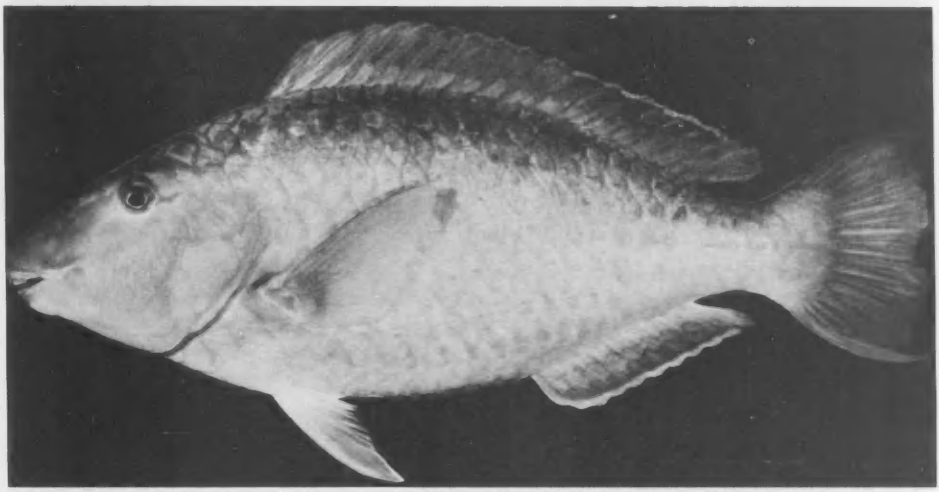

FIGURE 45.—*Hipposcarus harid,* 282 mm SL, Rangiroa, Tuamotu Archipelago.

Of four specimens, 340-412 mm SL, 1.3-1.8 kg, obtained at Enewetak, three were nontoxic, and one produced a reaction of 1.

Reporting on the stomach contents of *Cetoscarus bicolor, Scarus sordidus,* and seven unidentified species of *Scarus* in the Marshall Islands, Hiatt and Strasburg (1960) concluded that they fed mainly on live coral. This is contradictory to the investigation of scarid food habits by Wood-Jones (1910), Choat (1966), Randall (1967, 1974), Rosenblatt and Hobson (1969), and Hobson (1974). Randall (1974), however, presented evidence that the largest of the parrotfishes, *Bolbometopon muricatus,* feed heavily on living coral. Also Glynn et al. (1972) listed three scarids as coral predators off the Pacific coast of Panama.

Scarus gibbus Rüppell (Figure 46): The name *Scarus microrhinos* Bleeker has generally been used in the Pacific for this species (Schultz 1958), and it is under this name that its toxicity has been reported (Halstead 1967). Smith (1959) resurrected the name *Scarus gibbus* Rüppell for the Red Sea form of this species, though he still recognized *S. microrhinos*. Schultz (1969) placed four nominal species, including *S. microrhinos*, under the one name *S. gibbus*. The large males are readily distinguished by the near-vertical anterior profile of the head. Other useful characters for distinguishing the species are four median predorsal scales, three rows of scales on the cheek, and 16 or 17 pectoral rays.

Of 19 specimens, 326-414 mm SL, 1.05-2.8 kg, speared from Enewetak, only 1 of 410 mm (2.3 kg) was slightly toxic (mongoose reaction of 1).

Scarus rubroviolaceus Bleeker (Figure 47): This parrotfish was selected as the type-species of a new genus, *Scarops,* by Schultz (1958) principally on the basis of its having a single enlarged row of teeth on each upper pharyngeal bone. This genus, however, was not recognized by Rosenblatt and Hobson (1969). The primary phase of *S. rubroviolaceus* is reddish with small blackish spots and short streaks on the scales; the terminal male phase (the nominal *Pseudoscarus jordani* Jenkins and *Callyodon africanus* Smith were based on this form) is complexly colored, but mainly purplish on the anterior part of the body and abruptly green posterior to about the base of the seventh dorsal spine (this bicolored effect more evident in live than on freshly dead specimens); the head is mainly blue-green, shading to orange-yellow on the opercle, with transverse bands of turquoise and salmon on the lips and chin. There are generally 6 median predorsal scales, 3 rows of scales on the cheek, and 15 pectoral rays.

Like the other species of *Scarus*, *S. rubroviolaceus* is closely tied to coral reefs. It ranges from east Africa to the tropical eastern Pacific. Although this species has not been reported as poisonous, it would seem to have the same potentiality of causing ciguatera as other parrotfishes which may be toxic.

Three specimens, 355-370 mm SL, 1.4-1.6 kg, were obtained from Enewetak in order to test for possible toxicity. None were toxic.

Rosenblatt and Hobson (1969) wrote, "All of the eastern Pacific species of *Scarus* feed by scraping algae from the surface of rocks. We did not see evidence that they bit off pieces of coral...." *Scarus rubroviolaceus* is one of the four species they studied. Glynn et al. (1972), on the other hand, included *S. rubroviolaceus* among the three scarids they regarded as coral predators from observations off Panama.

Acanthuridae (Surgeonfishes)

Acanthurus xanthopterus Cuvier and Valenciennes (Figure 48): This is the largest member of

FIGURE 46.—*Scarus gibbus*, 417 mm SL, 2.8 kg, Tahiti, Society Islands.

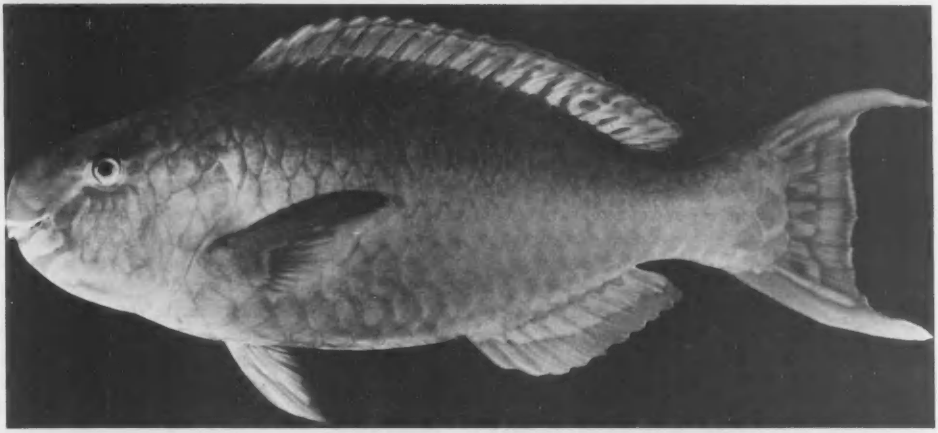

FIGURE 47.—*Scarus rubroviolaceus*, 355 mm SL, 1.35 kg, Enewetak, Marshall Islands.

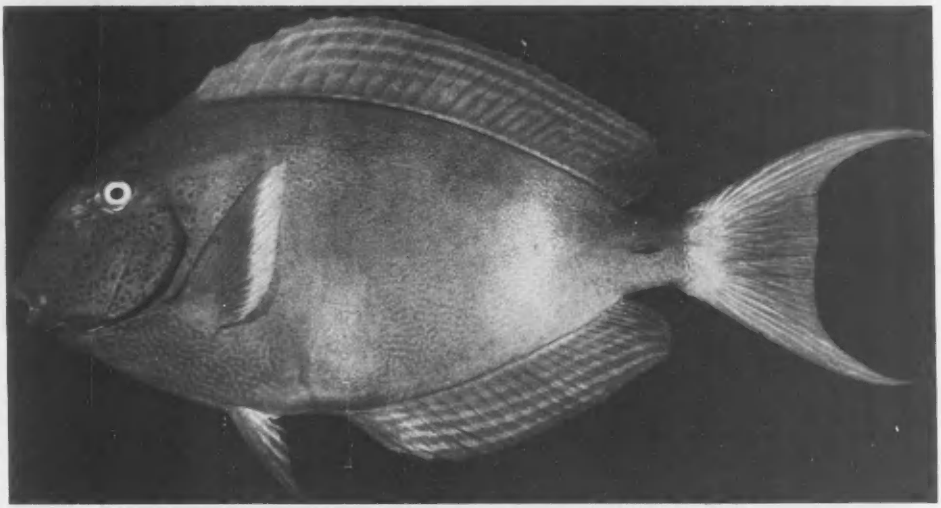

FIGURE 48.—*Acanthurus xanthopterus*, 400 mm SL, 2.3 kg, Enewetak, Marshall Islands.

the genus *Acanthurus*. It is one of a complex of species with a gizzardlike stomach. In the Marshall Islands it could only be confused with *A. mata*, also a large species. The outer third of the pectoral fins of *A. xanthopterus* are yellowish (fins uniform brown on *A. mata*), and there are about 4 lengthwise bands in the dorsal fin (about 8 in the fin of *A. mata*); there are fewer gill rakers (16-22 for *A. xanthopterus*, compared with 21-25 for *A. mata*). This species is distributed from east Africa to the eastern Pacific. It occurs more in lagoons and bays than exposed outer reef areas, and it ranges into deeper water than other *Acanthurus* in general. Also it ventures farther from the cover of coral reefs than other species. Schultz in Schultz and collaborators (1953) used the name *Acanthurus fuliginosus* Lesson for this fish, but there is no basis for equating it to Lesson's illustration and description, as explained by Randall (1956). The junior synonym *Teuthis crestonis* Jordan and

Starks was created for the species from Mexico.

Two specimens, 423 and 425 mm SL, 2.7 kg, were obtained from Enewetak for the assay of toxicity. Neither were toxic.

Hiatt and Strasburg (1960) examined the stomachs of four specimens from Enewetak, two of which were empty. The other two contained short filaments of algae with much sand, hydroid hydrocaulus, and wood splinters (probably from grazing on pilings). Jones (1968) classified *A. xanthopterus* as a grazer on diatoms and detritus in sand patches. That it will take animal food when the opportunity arises was aptly shown by Helfrich and Banner (1963) who used this species to induce ciguatera toxicity by feeding the poisonous flesh of *Lutjanus bohar*.

Ctenochaetus striatus (Quoy and Gaimard) (Figure 49): This surgeonfish is much the most common of the four species of the genus that occur in the Marshall Islands. It is, in fact, one of the most abundant reef fishes throughout the Indo-West Pacific region (though not Hawaii). The genus is named for its comblike teeth which are numerous, slender with expanded incurved tips, and flexible in the jaws. Randall (1955b) has differentiated *C. striatus* from the other species by having 5-7 denticulations on the expanded distal tips of the upper teeth, the highest average number of dorsal and anal soft rays (modally 29 dorsal rays and 26 or 27 anal rays), and a lunate caudal fin.

Bagnis et al. (1968) reported that surgeonfishes (particularly *C. striatus*) are responsible for 65% of the cases of ciguatera in Tahiti. There are three reasons for this: 1) the abundance of *C. striatus*, 2) its good-eating quality, and 3) the knowledge that the symptoms will be mild if ciguatera is incurred.

Bagnis (1968) documented the great variation in the symptoms of ciguatera in French Polynesia. He noted that digestive and neurologic symptoms predominated among those patients who had ingested surgeonfishes.

Yasumoto et al. (1971) determined that there are two principal toxins in *C. striatus*, one of which is fat soluble and chromatographically identical with ciguatoxin, and the other is water soluble. The latter was found only in the liver and gut contents. In a few specimens from Tahiti a different fat-soluble toxin and a different water-soluble toxin were detected.

In order to determine if more than one toxin is present in *C. striatus* in the Marshall Islands, 22 adult specimens were speared on lagoon reefs of

FIGURE 49.—*Ctenochaetus striatus*, 94 mm SL, Enewetak, Marshall Islands.

Enewetak and sent frozen to the Laboratory of Marine Biochemistry of the University of Tokyo. The specimens, which weighed from 130 to 230 g each, were pooled in groups of three (four for one group). The flesh and the viscera were separated for each group, and the gut contents of all groups were pooled. Fat-soluble and water-soluble fractions were prepared and injected intraperitoneally into mice at doses of 4,000, 2,000, and 1,000 μg/g. Two mice were used for each dose. If the mice were not killed by a dose of 4,000 μg/g within the observation period of 48 h, the preparation was regarded as nontoxic. If they were killed by a dose of 1,000 μg/g, it was classified as strongly toxic, at 2,000 μg/g moderately toxic, and at 4,000 μg/g weakly toxic. The results were reported in a letter by the late Yoshiro Hashimoto, then the Director of the Laboratory. None of the preparations were strongly toxic. All the preparations from the flesh were nontoxic. Four of the seven fat-soluble preparations of the viscera were moderately toxic, one was weakly toxic, and one nontoxic. Five of the seven water-soluble fractions from the viscera were weakly toxic and the remaining two nontoxic. Both the fat-soluble and the water-soluble preparations of the pooled gut contents were moderately toxic.

The food habits and mode of feeding of *C. strigosus* from the Hawaiian Islands were investigated by Randall (1955b); underwater observations of *C. striatus* indicate that its feeding is essentially the same. These fishes are detritus feeders. From a near-vertical position (if the bottom is horizontal) about 15 mm above the substratum, the fish move abruptly downward with mouth open. The lips and teeth scrape over the surface at the same time that suction is initiated. The soft detrital material and fine inorganic sediment are ingested. If coarse particles of sand are picked up, they are forcefully ejected. The stomach contents of seven adults of *C. strigosus* from Hawaii consisted of inorganic sediment (up to 90% by volume); fragments of red, green, and blue-green algae; diatoms; and unidentified soft organic material. In an aquarium experiment *C. strigosus* was unable to feed on an intact thallus of the filamentous alga *Polysiphonia* sp. When the same algae was finely fragmented and placed on the bottom, it was readily consumed.

Balistidae (Triggerfishes)

Pseudobalistes flavimarginatus (Rüppell) (Figure 50): This is one of three large species of triggerfishes that occur in the Marshall Islands. It may be distinguished from other balistids by the following characters collectively: the second dorsal and anal fins elevated anteriorly, five or six rows of spines on the caudal peduncle, no scales on the cheek (of adults), caudal fin of adults emarginate, and yellowish margins on the median fins. Woods in Schultz and collaborators (1966) failed to list this species from the Marshall Islands, but the color plate in Hiyama (1943, pl. 22, fig. 61) and the study of Hiatt and Strasburg (1960) clearly indicate its presence there. Hiatt and Strasburg stated that it is solitary, uncommon, and occurs on lagoon and interisland reefs in quiet water of 10-30 ft (3.1-9.1 m) deep. Although Hiyama wrote that this fish was not regarded as poisonous in the Marshalls, other records (Halstead 1967) demonstrate its capacity for causing ciguatera. It is one of the nine species of fishes forbidden to be sold in the fish market in Papeete, Tahiti (Bagnis 1968).

Two specimens, 465 and 535 mm SL, weight not taken, were collected in Bikini. Neither was poisonous.

Clark and Gohar (1953) reported pieces of branched coral (*Stylophora*) 2-3 cm long in the stomach of a specimen 440 mm SL from the Red Sea. Hiatt and Strasburg (1960) examined two stomachs from the Marshall Islands. They found the crustacean *Lydia annulipes* and isopods, crushed gastropods including *Oliva* sp., foraminifera, and colonial tunicate fragments.

The stomach and gut contents of only two specimens were obtained for the present study. One of 254 mm SL from the Red Sea was empty. The second of 390 mm SL from Tahiti had eaten *Diadema*.

Balistoides viridescens (Bloch and Schneider) (Figure 51): This is another large triggerfish for which there have been a few records of toxicity. It shares the elevated anterior part of the second dorsal and anal fins and the rows of spines on the caudal peduncle with *P. flavimarginatus*, but is differentiated by having its cheek totally scaled and its caudal fin rounded to slightly double emarginate as an adult; also the margins of its median fins are broadly blackish. It ranges from the Red Sea to eastern Oceania. It occurs in both lagoons and outer reef slopes. Like other triggerfishes, it has a favorite hiding place in the reef into which it wedges itself when threatened.

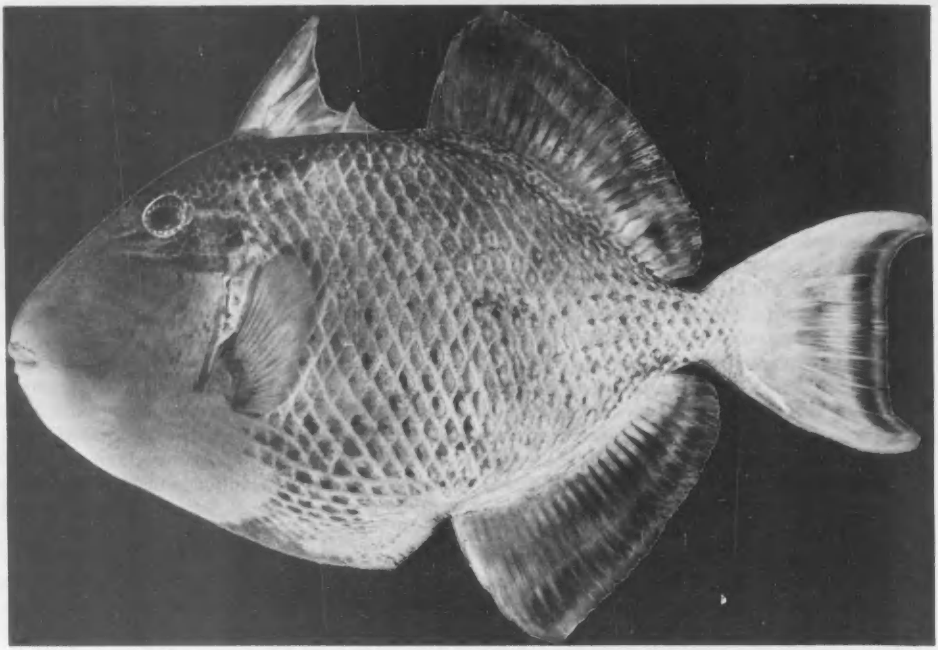

FIGURE 50.—*Pseudobalistes flavimarginatus*, 265 mm SL, Palmyra, Line Islands.

A single specimen, 456 mm SL, 4.5 kg, from Enewetak was nontoxic.

The stomach and gut contents of four specimens, 278-525 mm SL, from the Society Islands and the Red Sea were examined. Echinoids, including *Diadema*, *Echinometra*, and spatangoids, were the main items of diet, but pelecypods, crabs, polychaete tube worms, gastropods, chitons, foraminifera, and algae and detritus were also present.

DISCUSSION AND SUMMARY

As mentioned in introductory remarks, the initial testing for level of ciguatera at both Enewetak and Bikini revealed only an occasional toxic fish among the species responsible for most cases of this type of poisoning in the Pacific. As expected, the toxic individuals were invariably adults of moderate to large size for the species. A decision was then made to concentrate the fishing effort on the larger individuals of the species most often implicated in ciguatera. These dangerous species are, in general, not common. They are at or near the peak of the well-known "pyramid of numbers," i.e., the reduction in number of individuals one encounters analyzing the populations in successive steps up the food chain. Consequently, much more effort was expended in catching not only these fishes but just the larger individuals of these species. Also, it is for this reason that some relatively common species such as *Lutjanus fulvus* and *Adioryx spinifer* are represented by few individuals in this report and others such as the smaller species of groupers of the genera *Epinephelus* and *Cephalopholis* were not collected. In highly toxic sectors these species can be poisonous, though even there the incidence is low.

A total of 551 specimens of 48 species were tested from Enewetak and 256 specimens of 23 species from Bikini. In addition, 12 adult specimens of *Lutjanus bohar* from Rongelap were tested, one of which was toxic at the 5 level. The results of the testing of fishes from Enewetak are summarized in Table 1, and for Bikini in Table 2; 37.3% of the fishes from Enewetak gave a positive reaction for ciguatoxin, and 19.7% of those from Bikini.

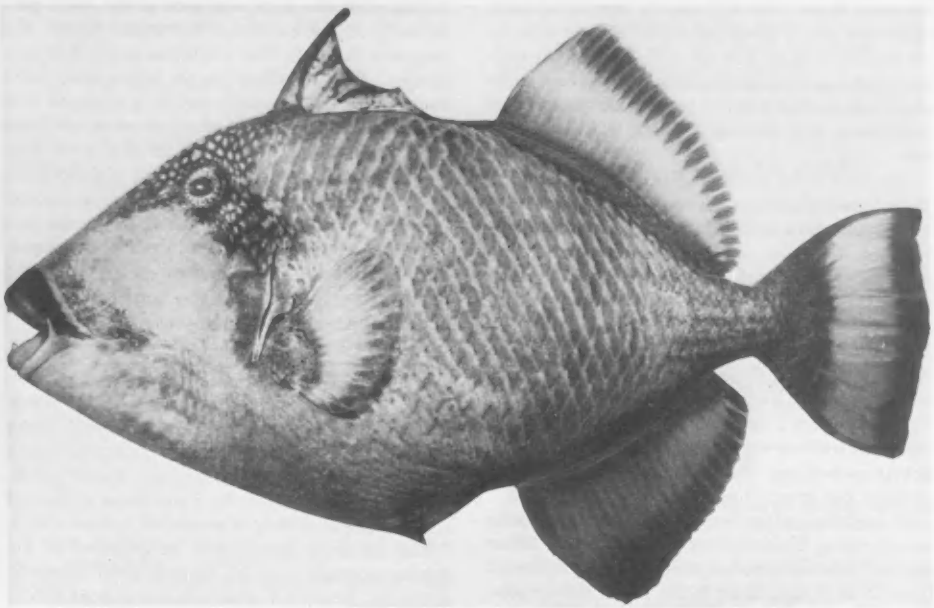

FIGURE 51.—*Balistoides viridescens*, 456 mm SL, 4.5 kg, Tetiaroa, Society Islands.

It must be emphasized that liver and viscera of the suspect fishes were used in the mongoose feeding tests (except for sharks) and not flesh. Because of the much higher level of ciguatoxin in the internal organs than in muscle tissue, low-level toxicity (indicated by mongoose reactions of 1 or 2) from liver and viscera would probably not result in a detectable level of toxin if flesh from these fishes had been used in the tests. When the percentage of toxicity is computed for the reactions 3-5 (it is this level at which a human eating the flesh of these species might be expected to fall ill with ciguatera), the percentage of toxic fishes drops to 16.2 for Enewetak and 1.4 for Bikini.

When one considers the effort directed almost entirely to the worst offenders in ciguatera, the level of toxicity at Enewetak must be regarded as relatively low and that of Bikini decidedly so. Most of these fishes are avoided as adults by islanders in Oceania regardless of the area of capture. Therefore it is concluded that the returning residents to Enewetak and Bikini need not fear at this time any unexpected threat of ciguatera at their atolls.

Only eight species of fishes produced reactions of 4 or 5 in the test animals; that is, severe illness or death: *Lycodontis javanicus*, *Cephalopholis argus*, *Epinephelus hoedtii*, *E. microdon*, *Plectropomus leopardus*, *Aprion virescens*, *Lutjanus bohar*, and *Lethrinus kallopterus*. Had more specimens of *Sphyraena barracuda*, *Caranx ignobilis*, and *Cheilinus undulatus*, particularly of large size (none of the specimens taken during this survey approached the maximum size), been collected, then they may be expected to be included in the above list (in view of their reputations for causing ciguatera in other areas).

The moray *Lycodontis javanicus* was clearly the most toxic of all the species tested, with all individuals producing a reaction of 2 or more in mongooses and one-third of them the lethal 5.

Randall (1958) analyzed the kinds of fishes which have caused ciguatera in terms of habitat, mode of life, and food habits. These species are shore fishes associated with reefs. Usually they are bottom-dwelling generally in < 60 m, but they may be semipelagic open-water forms that range into the reef habitat to feed. They may be carnivorous or they may feed on benthic algae or detritus. Of the carnivores, those that prey heavily on reef fishes are the most prone to be poisonous,

whereas those that eat mainly benthic crustaceans the least. Fishes that feed wholly or primarily on plankton are not apt to be toxic. Some mollusk and echinoid feeders may cause severe cases of ciguatera. The level of toxicity among benthic herbivores and detritus feeders is consistently low.

The food-habit studies of this survey support these generalizations. Seven of the eight most toxic species are piscivorous. The one other, *Lethrinus kallopterus*, appears to feed mainly on echinoids and mollusks. No specimens of *Lutjanus fulvus*, *Epinephelus socialis*, and *Adioryx spinifer* were found to be toxic (although relatively few specimens were collected); these feed more on crustaceans than fishes. Among the herbivores tested, only two individuals of *Scarus* and one of *Kyphosus* gave a reaction of 1. A water-soluble toxin as well as ciguatoxin were found in the detritus-feeding surgeonfish *Ctenochaetus striatus*, but in small amounts.

The relatively low level of ciguatoxin in sharks is surprising. Because they feed heavily on fishes and are believed to be long-lived, one might expect them to be as ciguatoxic as the larger moray eels. The tropical species of sharks are not as widely eaten as bony fishes. If they were, no doubt more cases of ciguatera would be attributed to them. The species of *Carcharhinus* appear to prey to a significant degree on pelagic fishes, and when they do feed on reef-dwelling species, they seem to take many plankton-feeding forms. This may in part explain their apparent relatively low level of ciguatoxin. Still another possibility is that sharks may not accumulate as much ciguatoxin in their tissues as bony fishes.

Because ciguatera can be highly localized to certain reefs or even sectors of reefs, the fish collecting was carried out at many different locations at the atolls. No one area was detected as having a notably higher level of toxicity.

Many of the most dangerous ciguatoxic species are roving predators. Examples are the barracudas, jacks, dogtooth tuna, emperors, and, to a lesser extent, the snappers. They can be caught at a different area from which they acquired most of their toxicity. The strong localization of ciguatera occurs more where the level of toxicity is high and the smaller more resident species are poisonous. Our fishing has not been sufficiently extensive to demonstrate minor differences in the incidence of ciguatera with locality.

At Enewetak most of the fishing was undertaken on the southern part of the atoll, particularly in the vicinity of Enewetak Island, the largest of the atoll. This island had the largest population of Marshallese people before they were evacuated from the atoll, and it is expected that it will have the largest number when all have been repatriated. Also it is in this area that most of the long-term disturbances of the marine environment, such as the dumping of unwanted material, have taken place. It is fortunate that ciguatera, though more in evidence at Enewetak than at Bikini, is not a major problem as might have been predicted from the impact of western man on the atoll.

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The testing of the toxicity was carried out by James Murphy and Lambert Yamashita at the Hawaii Institute of Marine Biology of the University of Hawaii, under the direction of A. H. Banner, except for the last sampling in May 1978 for which an initial screening was made by Yoshitsugi Hokama of the Department of Pathology, University of Hawaii, by radioimmunoassay (Hokama et al. 1977). The higher reactions were then confirmed by mongoose feeding at the Bernice P. Bishop Museum by Arnold Y. Suzumoto.

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CALLINECTES (DECAPODA: PORTUNIDAE) LARVAE IN THE MIDDLE ATLANTIC BIGHT, 1975-77[1]

PETER O. SMYTH[2]

ABSTRACT

Distribution of *Callinectes* larvae in surface (neuston) and subsurface shelf waters in the Middle Atlantic Bight was determined from quarterly zooplankton collections taken during a 2-year study. Observations confirmed the presence in offshore waters of a large larval pool from which recruitment may take place. Larvae were predominantly late zoeae and megalope, with peak abundances in late summer collections reaching 16,000 per 100 m^3 in neuston collections. During summer, crab larvae were distributed across the shelf with the majority at 10-80 km offshore. Abundances were significantly greater in neuston than subsurface zooplankton collections and generally greater in neuston collections taken at night. Water temperature and distance from shore were factors most closely correlated with abundance of larvae in the neuston. Megalopae of *Callinectes* were present at outer shelf stations in winter and spring and together with megalopae of *Portunus* and other forms were of southern origin. Based on experimentally determined temperature-salinity preferences reported in the literature for *Callinectes* larvae, metamorphosis may be delayed in cooler offshore waters, thus increasing chances of long-range transport.

The community of organisms of the surface layer (the neuston[3]) has received increasing attention in terms of sampling problems and possible ecological significance. Zaitsev (1970) described the neuston as consisting chiefly of early developmental stages of fishes and invertebrates. Berkowitz (1976) and Morris (1975), however, found oceanic neuston faunistically impoverished in comparison with zooplankton of the immediate subsurface. Few studies of the neuston of shelf and shallow waters exist; preliminary indications are that the zooplankton of the surface waters of the continental shelf are at least quantitatively enriched (Grant[4]).

Callinectes, euryhaline members of the predominantly marine Portunidae, spawn along the shore of open oceans and in mouths of inlets and estuaries. Larval development occurs in shelf waters, with probable return inshore by megalopae and juveniles (Williams 1965, 1971, 1974; Costlow 1967; Tagatz 1968). *Callinectes* megalopae have been reported offshore in shelf waters (Nichols and Keney 1963; Dudley and Judy 1971); retention in shelf waters and subsequent transport of megalopae have been proposed as mechanisms in dispersal, widespread distribution, and maintenance of genetic continuity in the species (Costlow 1967; Williams 1971, 1974; Cole and Morgan 1978).

Callinectes larvae, at least zoeae, have surface affinities (Tagatz 1968; Dudley and Judy 1971; Sandifer 1972), but megalopae have generally been less numerous in collections than zoeae and limited to bottom samples (Tagatz 1968; Sandifer 1972; Goy 1976). Williams (1971), however, reported *Callinectes* megalopae to be active in estuarine surface waters at night.

With the widespread distribution and known abundance of *Callinectes* adults and the accepted migratory sequence of developmental stages (inshore-offshore-inshore), the reported abundance of late stage larvae is surprisingly low. Furthermore, the existence in shelf waters of a *Callinectes* larval pool from which recruitment to estuaries may occur is based on relatively few studies and limited sampling.

This paper reports the identification, distribution, and abundance of *Callinectes* larvae in neus-

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[2]Virginia Institute of Marine Science and School of Marine Science, the College of William and Mary, Gloucester Point, VA 23062.

[3]Neuston has generally been defined operationally as the community of organisms sampled by gear specifically designed to sample the surface layer. The term is used in that sense in this paper. For a review of numerous terms associated with the surface layers, see Banse (1975).

[4]Grant, G. C. 1977. Middle Atlantic Bight zooplankton: seasonal bongo and neuston collections along a transect off southern New Jersey. Spec. Rep. Appl. Mar. Sci. Ocean Eng., Va. Inst. Mar. Sci. 173, 138 p.

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ton and subsurface water column collections from shelf waters in the Middle Atlantic Bight. My objectives specifically were to: 1) determine whether a reservoir of *Callinectes* larvae, particularly megalopae, exists in shelf waters; 2) determine abundance relationships between *Callinectes* larvae in neuston and water column samples; 3) examine the role of certain environmental factors (e.g., temperature, salinity, location) in the distribution and abundance of these larvae; 4) assess the role of *Callinectes* megalopae in larval recruitment and dispersal in view of my findings and results of laboratory studies of temperature-salinity tolerances of larvae; and 5) examine interaction of the developmental migratory sequence, biogeography, and evolutionary history of *Callinectes*.

METHODS

Zooplankton collections were made as part of a 2-yr survey (Table 1) conducted by the Virginia Institute of Marine Science (VIMS) for the Bureau of Land Management (1975-77). This study was designed to provide ecological information prior to drilling for oil on the Middle Atlantic Bight continental shelf. In addition to zooplankton studies the survey included studies of benthic and epibenthic communities and the physical, chemical, and geographical oceanography of the shelf and overlying waters.

During the first year, six stations were occupied seasonally (quarterly) on a transect across the shelf off Atlantic City, N.J. (Figure 1; Table 2: C1, D1, N3, E3, F2, J1). Zooplankton in the water column was sampled at night by paired, double oblique tows with 60 cm diameter, opening-closing bongo nets (McGowan and Brown[5]) (505 μm and 202 μm mesh). Bongo nets were metered (General Oceanics, Inc. flowmeters[6]) and were closed during passage through the surface layer. Neuston was sampled every 3 h over a 24-h period with a neuston net designed at Woods Hole Oceanographic Institution. This sampler consisted of two hydrodynamically-shaped, foam-filled floats connected by an endless fiber glass band (Grant[7]). The mouth of the net was 1.0 m wide, and in calm water the gear sampled approximately the upper 12 cm of the water column. However, the net appeared to sample, on the average, less than the upper 12 cm due to sea conditions and towing characteristics of the ship and sampler. Calculated volumes were based on a 12 cm sample depth and were thus overestimated, resulting in underestimation of

TABLE 1.—Dates for cruises in the Middle Atlantic Bight, 1975-77, over which *Callinectes* larvae were sampled.

Season	First year		Second year	
	Cruise	Date	Cruise	Date
Fall	01W	23-30 Oct. 1975	05W	5-28 Nov. 1976[1]
Winter	02W	5-16 Feb. 1976	06W	20 Feb.-6 Mar. 1977
Spring	03W	8-16 June 1976	07W	18-28 May 1977
Summer	04W	1-9 Sept. 1976	08W	19-29 Aug. 1977

[1]Cruise split into two legs.

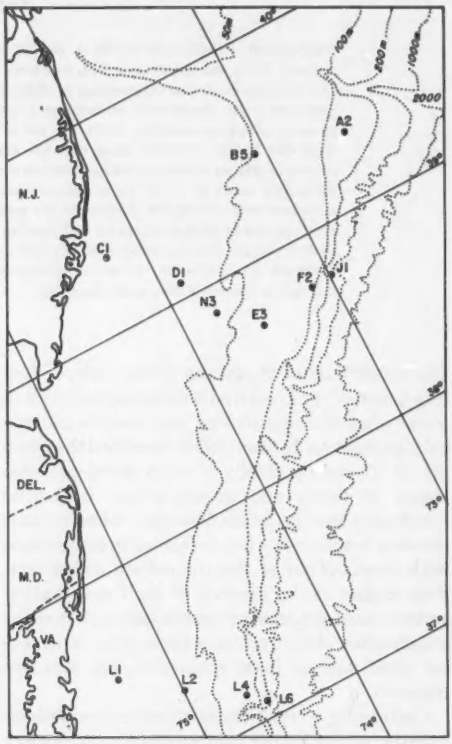


FIGURE 1.—Study area and sampling stations for surface and subsurface zooplankton in the Middle Atlantic Bight, 1975-77. Stations L1, L2, L4, L6, B5, A2 were sampled only during the second year of the study; C1, D1, N3, E3, F2, J1 were sampled both years.

[5]McGowan, J. A., and D. M. Brown. 1966. A new opening-closing paired zooplankton net. Univ. Calif., Scripps Inst. Oceanogr. Ref. 66-23, 56 p.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[7]Grant, G. C. 1979. Middle Atlantic Bight zooplankton. Spec. Rep. Appl. Mar. Sci. Ocean Eng., Va. Inst. Mar. Sci. 192, 236 p.

TABLE 2.—Station data for zooplankton collections in the Middle Atlantic Bight, 1975-77.

Station	Location		Distance from shore (km)	Bottom depth (m)
	Lat. N	Long. W		
A2	39°21.8′	72°31.8′	149	131
B5	39°28.3′	73°02.1′	93.6	62.6
C1	39°22.2′	74°14.9′	10.2	16.8
D1	39°04.7′	73°53.2′	56.5	37.2
N3	38°51.4′	73°44.8′	83.4	44.7
E3	38°41.2′	73°32.5′	112	59.5
F2	38°44.4′	73°09.2′	132	108
J1	38°44.2′	73°00.7′	141	355
L1	37°31.1′	75°18.3′	31.5	22.3
L2	37°20.1′	74°58.6′	65.8	41.3
L4	37°08.1′	74°36.8′	105	94.6
L6	37°04.4′	74°33.1′	113	322

larval densities. Tows were of 20-min duration except when large abundances of neuston required premature termination of a tow. The net was metered beginning with the June 1976 cruise; before that cruise, sample volumes were estimated on the basis of a standard 20-min tow. Tows were made from an extended boom alongside the ship at speeds of 1.5-2.5 kn.

During the second year two stations to the north and a transect to the south of the original transect were added. On each cruise neuston samples were taken over 24 h at nine stations (Figure 1; Table 2: A2, B5, C1, E3, J1, L1, L2, L4, L6). A single neuston tow was made at stations D1, N3, and F2 as a companion to bongo tows. Bongo tows were made at all 12 stations following the procedure used during the first year. In addition, replicate tows were made at stations A2, B5, and E3 (repeated tows of two bongo nets with paired 202 μm and 505 μm mesh nets). Three such replicate tows were made at night at each designated station.

Samples were preserved in a 4% solution of borax-buffered formaldehyde and seawater (Steedman 1976). In the laboratory, major taxonomic groups were quantitatively sorted from whole or split samples (Burrell et al. 1974). Decapods were sorted to species and identified (when possible) on the basis of published descriptions and taxonomic keys.

Megalopae of several taxa, including *Callinectes*, were reared aboard ship to juveniles. Several megalopae were removed from a sample and tentatively identified or identification characters noted. Megalopae were placed in plastic tackle boxes with 505 μm mesh bottoms and the boxes were floated in an aquarium filled with seawater taken in situ. Megalopae were fed *Artemia salina* nauplii and bits of fresh fish meat. Megalopae with the same characteristics as the megalopae used for rearing were fixed and preserved.

Abundance was expressed as number per 100 m^3; for graphical presentation and certain statistical procedures abundance was compressed by the transformation $\log_{10}(X + 1)$. Most statistical procedures were based on station means, with eight neuston collections per station. The distribution of sample means tends to normality as the sample size increases (Snedecor and Cochran 1967), and the logarithmic transformation tends to make variance independent of the mean (Sokal and Rohlf 1969). Based on the F-max test (Sokal and Rohlf 1969), untransformed abundances within stations were very heteroscedastic, while log-transformed abundances at stations with *Callinectes* larvae in at least six samples did not have unequal variances at $P<0.05$. Coefficients of variation for each station were reduced considerably by the log transformation, and abundances appeared better centered about the median based on "box and whisker" diagrams (Tukey 1977). The assumption of a multivariate normal distribution could not be tested for the data set. Significance levels for mulitvariate data are often difficult to interpret; therefore, significance levels, where indicated for parametric procedures, should be taken as a guide.

A larval stage index (LSI) similar to that of Manzi and Maddox (1976) was calculated for several larval types. The LSI is a point along the continuum of development from hatching (first zoea) to juvenile; the LSI characterizes the stage of an average individual of a given species in a sample. It is calculated as a weighted average, i.e.,

$$\mathrm{LSI} = \frac{\sum_{i=1}^{n} i S_i}{n \sum_{i=1}^{n} S_i}$$

where i = number of the developmental stage,
n = number of developmental stages, first zoeae through adult,
S_i = abundance of the ith stage.

The LSI is standardized and constrained in the interval 0.0-1.0 by the assignment of a stage number (1> the megalopa) to the adult stage. Thus, an LSI = 0.67 characterizes animals that have completed, on the average, about two-thirds of the developmental sequence from hatching to first crab. The LSI is, however, a measure of central tendency and does not indicate statistical dis-

persion. Based on Costlow and Bookhout (1959), *n* was set at 10 for eight zoeal stages, a megalopa, and an adult.

Comparisons between *Callinectes* abundance in neuston and bongo (surface vs. subsurface) collections at each station were made for: 1) maximum abundance for each gear type; 2) mean abundance of the consecutive pair of tows with the largest collective abundance; and 3) mean abundance for each gear type. Significance of differences for these means was determined by the Wilcoxon signed rank test (Wilcoxon 1945), a distribution-free method (Hollander and Wolfe 1973).

Comparisons between neuston and bongo collections are comparisons between abundances in a single "layer" and abundances integrated over the water column. Therefore, abundances in bongo collections represent mean abundances in the water column (excepting the surface) and do not indicate vertical distribution of the animals.

Diel patterns in neuston abundance during each cruise were represented by total numbers per 100 m^3 for each sampling time interval (3 h) summed over the stations in a cruise. To weight frequency as well as abundance during a single cruise, ranks were assigned to abundance during each time interval (lowest to highest) at each station. The rank sum of each time interval was calculated as the sum of the ranks during that time interval over all stations during a single cruise.

For neuston collections the relationship between mean abundance per station and environmental factors (temperature, salinity, station depth, and distance from shore) was examined. Data were analyzed using subprograms (multiple) Regression and Partial Corr (partial correlation) of the Statistical Package for the Social Sciences (SPSS, Nie et al. 1975). Relationships between abundance and factors were examined in terms of bivariate as well as multivariate distributions.

RESULTS

Identification

Callinectes zoeae were identified and staged on the basis of Sandifer's (1972) key and descriptions of laboratory-reared zoeae of *C. sapidus* (Costlow and Bookhout 1959) and *C. similis* (Bookhout and Costlow 1977). Key characters include: 1) relative length of the antennal exopodite (<⅓ protopodite length) and the presence of two unequal terminal setae on the antennal exopodite; 2) the presence of lateral projections on abdominal somites 2 and 3; 3) the presence of relatively long, sharply pointed posterolateral spines on abdominal somites 3-5; and 4) the presence of one dorsal and one lateral spine in each telson furca. Structure and setation of mouthparts and appendages were compared with published descriptions for further confirmation. The above characters effectively separated *Callinectes* zoeae from all other zoeal types in my collections. The planktonic material appeared to include seven or eight distinct zoeal stages after allowance for individual variation in certain structures, setal counts, relative lengths, etc. (e.g., the antennal endopodite "bud" denoting stage 5, which varied from little more than a swelling to a definite projection).

Identification of Portunidae megalopae was based on Kurata's (1975) list of familial and subfamilial (Portuninae) characters, which include the presence of sternal cornua (paired spines projecting posteriorly from the fourth sternal segment beyond the base of the fifth leg) (Figure 2), and the presence of paddlelike dactyls with long, hooked setae on the fifth pereopods.

Callinectes and *Portunus* megalopae were separated on the basis of the characters listed by Bookhout and Costlow (1974), which include the absence in *Callinectes* and the presence in *Portunus* of a ventral spine on the coxa of the second pereopod (Figure 2), and carpal spine(s) on the first pereopod.

My collections included numerous megalopae attributable to *Portunus*; all had a coxal spine on the second pereopod and a carpal spine on the first pereopod. The basischiopodite hook reported for

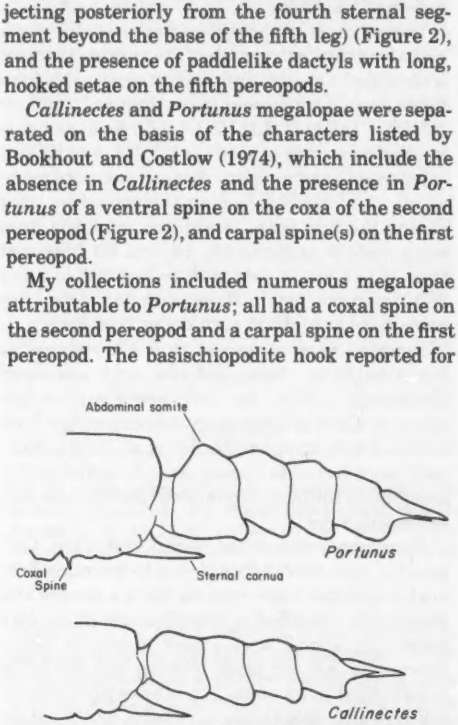


FIGURE 2.—Lateral profile including the abdomen of *Callinectes* and *Portunus* megalopae. Distinguishing characters are indicated. Sizes are not relative.

Portunus (Bookhout and Costlow 1974; Kurata 1975) and *Callinectes* (Costlow and Bookhout 1959; Bookhout and Costlow 1977) was present for all *Callinectes* and most, but not all, *Portunus* specimens.

The profile of abdominal somites was a more subjective, yet reliable, criterion for the separation of *Portunus* and *Callinectes* megalopae. In *Portunus* the dorsal surface of each somite, particularly the first, was noticeably raised, creating a "bumpy" profile; in *Callinectes* the profile was noticeably smoother (Figure 2). (See also Bookhout and Costlow 1974, fig. 11; 1977, fig. 11.) Although identifications were based on numerous characters, this particular criterion was consistent and reliable.

Carapace lengths (n = 418, $\bar{X}$ = 1.56, SE = 0.004 mm) of *Callinectes* megalopae (measured dorsally from the base of the rostrum to the posterior edge of the carapace) were slightly less than carapace lengths reported for *C. sapidus* ($\bar{X}$ = 1.65 mm) but considerably greater than lengths reported for laboratory-reared *C. similis* ($\bar{X}$ = 1.30 mm) (Bookhout and Costlow 1977).

I recognized no specific differences among *Callinectes* megalopae or zoeae; therefore, larvae referred to as *Callinectes* may represent more than one species. Abundance and known distribution of adults (Williams 1974) indicated that most, if not all, specimens were *C. sapidus*. Several small adult *C. similis*, however, were taken in neuston collections at station C1 in late October 1975.

The above characteristics used to separate *Callinectes* and *Portunus* megalopae were confirmed by specimens reared to the juvenile stage. *Portunus* juveniles were too small (<10 mm carapace width) for specific identification. One *Callinectes* megalopa developed to a juvenile stage tentatively identified as *C. sapidus*.

Distribution

Callinectes larvae were collected on six of eight cruises and were most abundant in late summer (Figure 3).

Mean abundance in neuston collections (n = 8) at a single station reached 3,100/100 m³ at L2 in August 1977; at this station abundance in a single neuston collection reached a peak of 16,000/100 m³. Abundance generally decreased offshore of the 50 m isobath during the summer-fall cruises (station J1 in August 1977 was an exception). During the second year, with additional stations, larvae were generally more abundant at stations on the most southern transect than at more northerly stations. Peak abundance often coincided with depressed LSI's inshore, evidence that reproductive activity inshore closely preceded the sampling periods. Except during the summer, larval populations consisted almost exclusively of late zoeae and megalopae, particularly in central and outer shelf waters. Collections of *Callinectes* during the fall of 1975 and winter and spring of 1977 comprised only megalopae.

Mean and maximum abundance (Figure 3; Table 3) was greater in neuston than in bongo collections except at three stations during summer 1977 (Figure 3). During winter 1977, occurrences were too few to be tested at the 0.05 confidence level by the signed rank test. On all other cruises during which *Callinectes* larvae occurred, abundance was significantly greater in surface than subsurface collections (Table 3).

Diel patterns in neuston abundance of *Callinectes* were not consistent over all cruises (Figure 4). A dawn peak in abundance was evident in summer 1976. Dusk peaks appeared in fall 1975 and possibly spring 1977. Total abundance was greatest during darkness (between sunset and

TABLE 3.—Comparison of surface and subsurface (neuston vs. bongo) abundance of *Callinectes* larvae, based on the signed rank test (Wilcoxon 1945). N denotes greater abundance in neuston, significance level indicated by asterisks (* = 0.05, ** = 0.01); P is the probability of a rank sum equal or greater under the null hypothesis of equal surface and subsurface abundance; fraction in parentheses: numerator is the number of occurrences in particular abundance category and denominator is the number of possible occurrences in abundance category.

Comparison	Season and year of collection					
	Fall 1975	Summer 1976	Fall 1976	Winter 1977	Spring 1977	Summer 1977
Maximum neuston vs. maximum bongo	N* P = 0.016 (6/6)	N* P = 0.016 (6/6)	N** P = 0.004 (8/12)	N P = 0.062 (4/12)	N* P = 0.016 (6/12)	N** P = 0.008 (12/12)
Maximum consecutive pair of neuston tows vs. bongos, mean	N* P = 0.016 (6/6)	N* P = 0.016 (6/6)	N** P = 0.008 (7/9)	N P = 0.125 (3/9)	N* P = 0.016 (6/9)	N** P= 0.004 (9/9)
Neuston vs. bongos, mean	N* P = 0.016 (6/6)	N* P = 0.016 (6/6)	N** P = 0.008 (7/9)	N P = 0.125 (3/9)	N* P = 0.016 (6/9)	N** P = 00.10 (9/9)

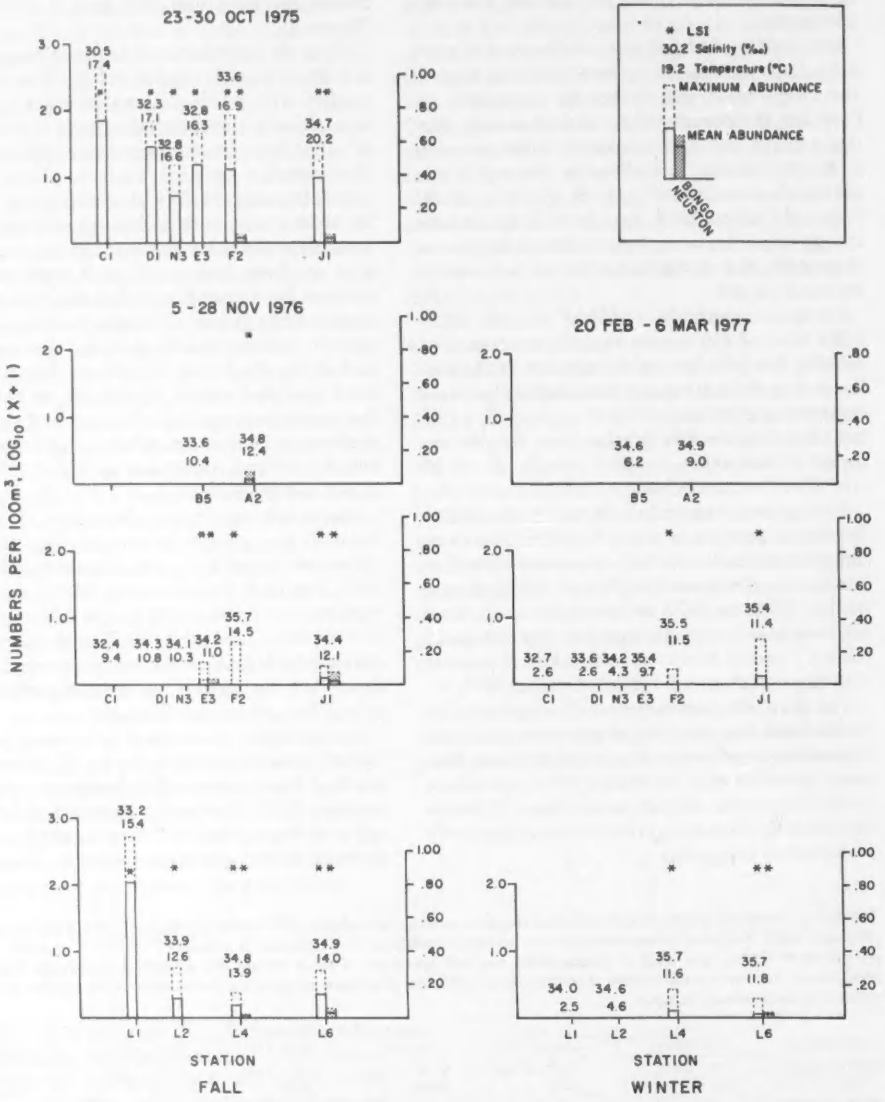
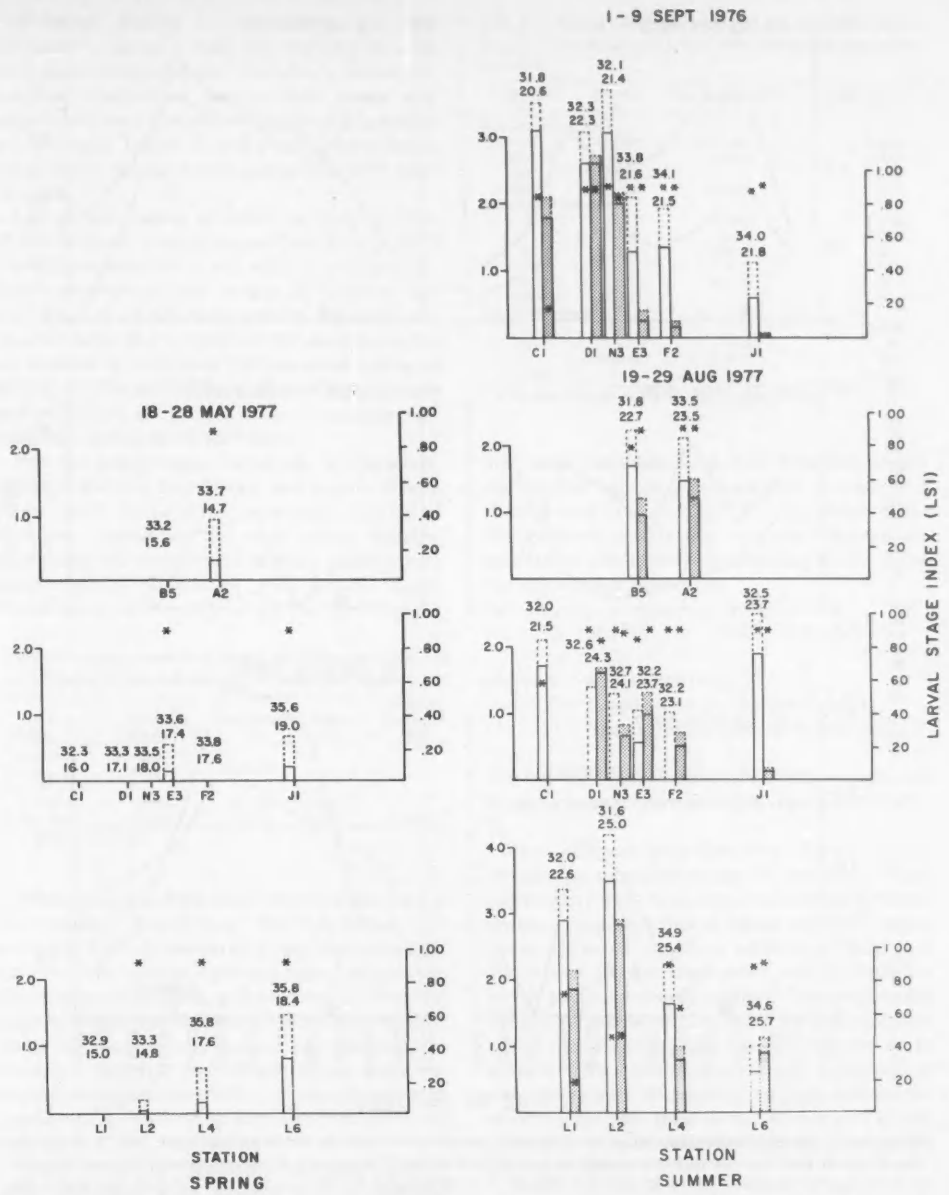


FIGURE 3.—Abundance and larval stage indices (LSI) of *Callinectes* larvae in surface and subsurface collections in



the Middle Atlantic Bight, 1975-77. Stations are ordered by increasing depth on a logarithmic scale within each graph.

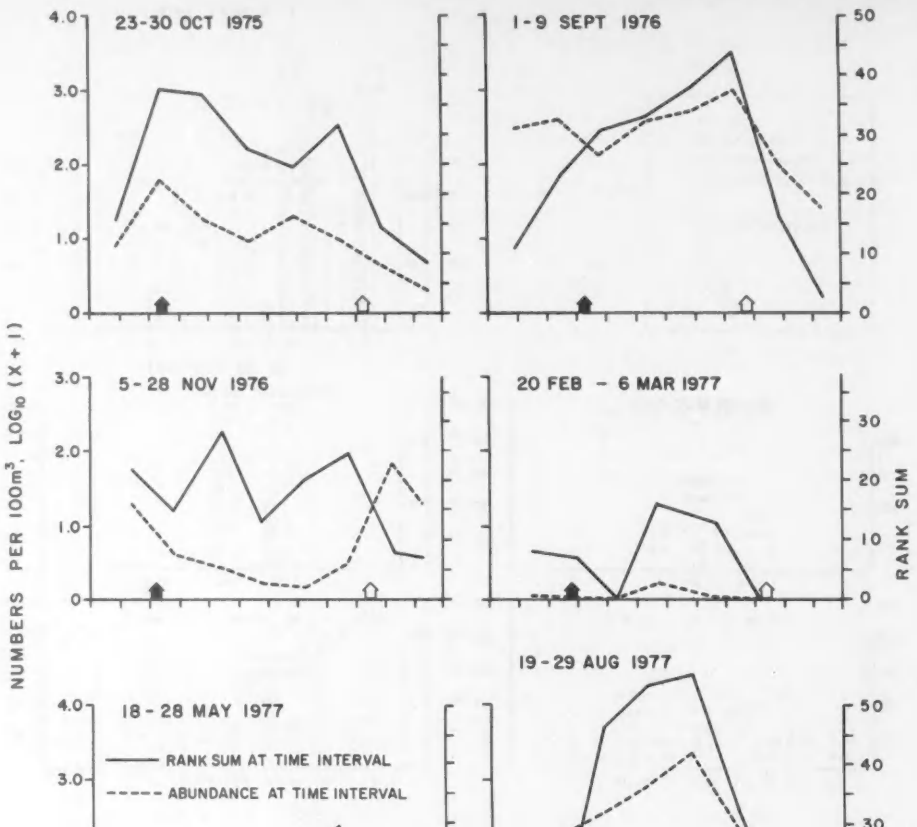


FIGURE 4.—Diel changes in abundance of *Callinectes* larvae in neuston collections in the Middle Atlantic Bight, 1975-77. Abundance (dashed line) for each time interval was averaged over the stations of a cruise. The rank sum for each cruise (solid line) was calculated by summing over all stations the ranks (lowest to highest) of the abundances at each time interval. (The rank sum weights the frequency of occurrence at each time interval.)

sunrise) on all cruises except fall 1976, when abundance was greatest during daylight hours. The rank sum, which weights both abundance and frequency of occurrence, indicated patterns of

diel change similar to diel patterns of total abundance—except during fall 1976. As distance from shore increased and abundance decreased, however, *Callinectes* larvae (late zoeae and megalopae) were generally collected at the surface only at night. Ten of 15, and 10 of 12 occurrences (megalopae) during winter and spring 1977 were at night.

Larvae were taken at salinities ranging from 30.5 to 35.8‰ and temperatures from 11.0° to 25.7° C (surface temperature and salinity); peak abundance occurred in the ranges 31.6-34.9‰ and 20.6°-25.7° C. Mean temperature, salinity, and distance from shore, weighted for abundance, for all neuston collections of *Callinectes* larvae were 22.9° C, 31.9‰, and 55.9 km. Plots of temperature and salinity vs. abundance indicated no clear relationships among these variables.

For the independent variables—temperature, salinity, distance from shore, and depth—simple (bivariate) correlation analysis indicated strongest correlation between mean neuston abundance per station and salinity and weakest correlation of abundance with bottom depth (Table 4).

TABLE 4.—Simple correlation matrix for surface abundance of *Callinectes* larvae and selected environmental variables.

Variable	Abundance ($\log_{10}[X+1]$)	Temperature (°C)	Salinity (‰)	Distance from shore (km)
Temperature	0.6260***			
Salinity	-0.7086***	-0.5133**		
Distance from shore	-0.5812***	-0.1695	0.6259***	
Bottom depth	-0.4024**	-0.1218	0.5621**	0.6261***

**$P<0.01$, ***$P<0.001$.

When considered together, the variables form a multivariate population. Partial correlation analysis (Table 5) indicated a very weak relationship between bottom depth and larval abundance for all second and third, and most first order correlations. Depth was, therefore, deleted from further analysis. Second order correlations among temperature, salinity, and distance from shore revealed strongest correlation of abundance with temperature, followed by distance from shore and salinity.

Based on partial correlation analysis, independent variables were entered into a multiple regression equation in the order temperature, distance from shore, salinity, and depth. These variables explained 66.0% of the variation in abundance (Table 6), the maximum possible for any linear combination of these variables. Depth contributed negligibly to explained variance, and salinity very little (Table 6). The regression equation containing only the variables temperature and distance from shore, explaining 62.4% of the variation in abundance, is

$$A = 0.1393 + 0.1124T - 0.0115D$$

where A = abundance ($\log_{10}[X + 1]$),
T = temperature in degrees Celsius,
D = distance from shore in kilometers.

TABLE 5.—Partial correlation coefficients for surface abundance $\log_{10}[X+1]$ of *Callinectes* larvae with selected environmental variables.

Temperature (°C)	Salinity (‰)	Distance from shore (km)	Bottom depth (m)
First order correlations:			
c[1]	-0.5787	-0.6182	-0.4214
0.4331	c	-0.2502	-0.0069
0.6577	-0.5434	c	-0.0606
0.6350	-0.6372	-0.4613	c
Second order correlations:			
c	c	-0.3969	-0.1240
c	-0.3051	c	-0.0627
c	-0.4514	-0.5017	c
0.5194	c	c	0.1135
0.4472	c	-0.2732	c
0.6578	-0.5493	c	c
Third order correlations:			
c	c	c	0.0378
c	c	-0.3815	c
c	-0.3013	c	c
0.5112	c	c	c

[1]c indicates variable which is controlled (effects removed).

The regression of abundance on temperature and distance from shore was highly significant (Table 7).

The temperature-distance from shore-abundance relationship for all cruises is summarized in Figure 5. Summer collections formed a unique group, distributed across the shelf. Abundance appeared relatively uniform at least to a distance of 100 km from shore, with a slight increase at the outermost stations. Temperature did not appear to be a limiting factor for these summer collections. Relationships are less clear for other seasons. Fall collections generally decreased in abundance with decreasing temperature and increasing distance from shore. Winter and spring collections formed groups which were limited to the outer shelf.

Cooccurring Decapods

Collections made during periods of peak abundance of *Callinectes* (in the summer) included

TABLE 6.—Variation explained by multiple regression of surface abundance ($\log_{10}[X + 1]$) of *Callinectes* larvae on temperature, distance from shore, salinity, and depth as estimated by the coefficient of determination (r^2). Data were entered in the order indicated in the Statistical Package for the Social Sciences (Nie et al. 1975) stepwise multiple regression procedure.

Temperature, distance from shore, salinity, depth			Salinity, temperature, distance from shore, depth		
Variable	r^2	Δr^2	Variable	r^2	Δr^2
Temperature (°C)	0.3919	0.3919	Salinity	0.5021	0.5021
Distance from shore (km)	0.6243	0.2324	Temperature	0.5955	0.0934
Salinity (‰)	0.6592	0.0350	Distance from shore	0.6592	0.0637
Bottom depth (m)	0.6597	0.0005	Bottom depth	0.6597	0.00049

TABLE 7.—ANOVA table for regression of surface abundance ($\log_{10}[X+1]$) of *Callinectes* larvae on temperature and distance from shore.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Total	41	37.23161	0.908088	
Regression	2	23.24224	11.62112	32.39773***
Residual	39	13.98937		

***$P \leq 0.001$.

peak abundances of inshore and estuarine genera such as *Uca* (zoeae and megalopae), *Emerita* (zoeae), *Palaemonetes* (zoeae), *Upogebia* (zoeae), *Libinia* (zoeae and megalopae), and *Ovalipes* (zoeae and megalopae). Few of the above were found beyond the inner shelf (Figure 1: C1, D1, L1). At offshore stations *Callinectes* larvae frequently occurred with larvae of shelf forms such as *Cancer*, which dominated neuston collections made in the spring. Megalopae and a few zoeae of *Portunus* usually occurred with *Callinectes*. Megalopae of *Ocypode quadrata* were ubiquitous across the shelf during summer 1977. Megalopae of *Dromidia antillensis* and other forms of southern origin often occurred at central and outer shelf stations.

DISCUSSION

Temperature-salinity tolerances of *Callinectes* larvae are available from several laboratory and field studies. Optimum temperature-salinity ranges, experimentally determined, for survival during zoeal development of laboratory-reared *C. sapidus* were 21-28‰, 19°-29° C (Sandoz and Rogers 1944) and 20-32‰ at 25° C (Costlow and Bookhout 1959). Sandifer (1972) collected *C. sapidus* zoeae in Chesapeake Bay in the range 15.7-32.3‰ (most at 20-30‰) and 14°-27.9° C (75% at 25°-26° C). Nichols and Keney (1963) found larvae (zoeae and megalopae) to be most abundant offshore (Florida-North Carolina) at 27.3°-29.1° C and least abundant at 14.3°-16.4° C.

Costlow (1967) reported survival of megalopae to first crab in temperature-salinity combinations of 15°-30° C, 5-40‰. Survival was similar at 20°, 25°, and 30° C, 10-40‰ (75% survival) and occurred at salinities as low as 5‰ at 25°-30° C. Survival in the lower salinity ranges (5-10‰) increased with increasing temperature to 95% at 30° C, 10‰. Survival in the upper salinity ranges (30-35‰) decreased from 95-100% at 25° C to 42-50% at 15° C. At 15° C larvae did not survive below 20‰, and at 15° C survival was highest at 35‰ (50%).

Costlow and Bookhout (1959) found zoeal development to require 31-49 days, with no significant difference in larval duration at salinities from 20.1 to 31.1‰ (at 25° C). Duration of the megalopal stage ranged from 5-11 days at 30° C (5-40‰) to 30-67 days at 15° C (20-40‰) (Costlow 1967). Costlow (1967) reported significant interaction between temperature and salinity only at 15° C. Larval duration at 35‰, 15° C was 37-56 days. Costlow (1967) did not rear larvae at temperatures <15° C and did not include a regression equation for extrapolation to lower temperatures.

Based on experimentally determined tolerances noted above, summer temperatures in the estuaries and inshore waters along most of the middle Atlantic and southeastern U.S. coast are sufficiently warm for completion of larval development. Metamorphosis of megalopae may occur during the warmer months at salinities found from offshore to upper estuaries. Greatest survival, however, is at higher salinities (30-40‰), and at 15° C occurs only in the range of oceanic salinities. Furthermore, at these oceanic salinities the duration of the megalopal stage increases as temperature decreases. Thus, megalopal life may be extended in the cooler, offshore water of the Middle Atlantic Bight, a conclusion supported by the presence of *Callinectes* megalopae at outer shelf stations (11°-12° C, 35-36‰).

Results of multivariate analysis of data were predictable (Figure 5; Tables 5-7). The importance of temperature (positive correlation) reflected the seasonal nature of spawning and development (in

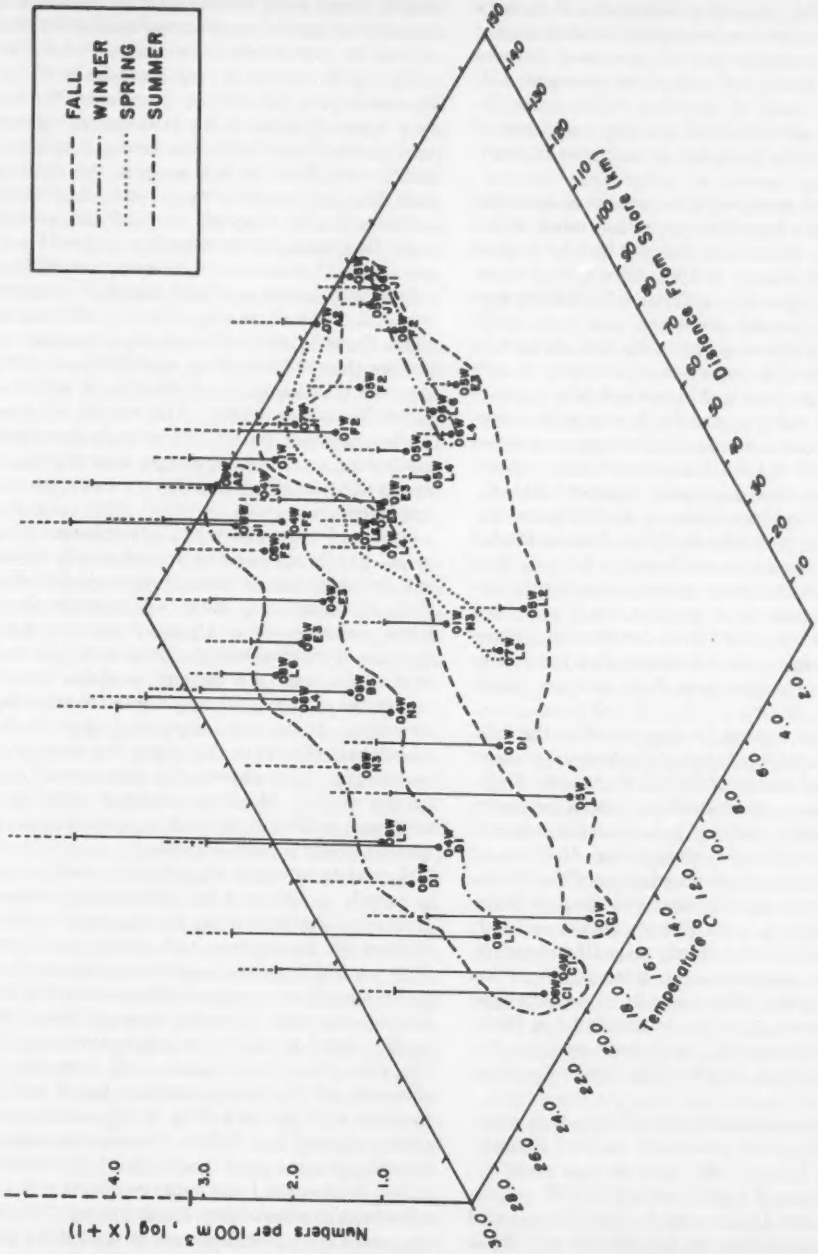


FIGURE 5.—Temperature-distance from shore-abundance diagram for *Callinectes* larvae in neuston collections in the Middle Atlantic Bight, 1975-77. Abundance is indicated on the vertical scale by a solid line for mean abundance and dashed line for maximum abundance. Stations (under cruise numbers) are grouped by season within broken lines.

summer). The secondary importance of distance from shore (negative correlation) was reflected in decreasing abundances with increasing distance from shore. Because all collections were made well within the range of optimum salinities for development, salinity could have been expected to contribute little to explained variation in abundance.

Results of multivariate analysis of data emphasize that a bivariate approach to multivariate data can be misleading. Salinity had the highest simple correlation (−0.7086; Table 4) with abundance. Consequently, in the usual SPSS stepwise multiple regression procedure (Nie et al. 1975) salinity would be entered as the first variable in the analysis. The proportion of variation (r^2, Δr^2) in abundance explained by temperature, distance from shore, salinity, and depth was quite in contrast to proportions of explained variance when salinity, rather than temperature, was entered first in the multiple regression equation (Table 6).

The relative importance of temperature, distance from shore, and salinity was best illustrated by partial correlation coefficients (Table 5). This procedure examines correlation between two variables when the effect of other variables is controlled. I recommend partial correlation as a preliminary step to multiple regression procedures and as more appropriate than bivariate procedures.

This paper reports for the first time the existence of a large population of *Callinectes* larvae in offshore shelf waters of the Middle Atlantic Bight. The presence of an offshore population, necessary to the accepted model of larval distribution, has had relatively little documentation. Nichols and Keney (1963) found advanced stages of *Callinectes* as far as 64-97 km offshore, with greatest abundance at stations 32 km offshore. Dudley and Judy (1971) reported zoeae, chiefly stage III and earlier, and a few megalopae at stations 10-13 km offshore. Tagatz (1968) reported a few megalopae as far upstream as 40 km in the St. Johns River, Fla., and Williams (1971) collected megalopae ". . . almost the entire length of the [North Carolina] estuary."

Abundance reported here (Figure 3) is somewhat less than that previously reported. Sandifer (1972) and Tagatz (1968) reported maximum larval abundance of 42,000 and 46,100/100 m^3, respectively, and Dudley and Judy (1971) reported maximum abundance of 105,000/100 m^3. These data, however, included few megalopae. Williams (1971) found considerably greater numbers of megalopae than did previous workers but reported abundance as numbers per sample (10's-1,000's).

My results confirm the reported affinity of *Callinectes* larvae, particularly megalopae, for surface layers. Previously Sandifer (1972) reported that 89.4% of the *Callinectes* larvae that he collected were from surface samples but reported only three occurrences of megalopae, all in bottom samples. Dudley and Judy (1971) found, overall, more *Callinectes* larvae in surface (1.0 m) than in subsurface (8.0 m) collections except at offshore (10-13 km) stations. They collected advanced zoeae (their last three stages) only at offshore stations. Tagatz (1968) collected more zoeae at the surface than at the bottom, and Williams (1971) reported *Callinectes* megalopae to be active at night in surface waters. The results of these studies, however, reflect differences in gear types, mesh sizes, and sampling design; gear specifically designed to sample surface layers was in no case employed.

Reasons for the affinity of *Callinectes* and other megalopae for the neuston are not readily apparent. Diel increases in abundance in night collections of neuston may indicate a negative phototropic response or possibly net avoidance in the daytime. Numerous holoplankters (copepods, etc.) exhibit the same diel pattern, and the upward movement of megalopae may be related to feeding strategies. It is not surprising that of the megalopae collected in this study, the Portunidae (swimming crabs) showed the strongest affinity for the neuston. Megalopae of other crabs, however, such as *Cancer*, *Ocypode*, and *Dromidia* also showed strong surface affinities.

Spatial distribution of plankton in shelf waters is largely determined by circulation patterns. With cross-shelf flow in the Middle Atlantic Bight offshore at the surface and onshore at depth (Bumpus 1973), coastal organisms in the surface layers would be transported offshore, with the possibility of return at depth. A coastal boundary layer, a band of trapped nearshore flow some 10 km wide, has been reported off New Jersey (Csanady 1976). Coastal boundary layers are associated with the upwelling of cold water as a consequence of the offshore movement of surface waters and subsequent thermocline tilt (Csanady 1976). Most coastal and estuarine larvae in my collections (species of *Uca*, *Palaemonetes*, *Libinia*, etc.) were infrequent seaward of station C1 and are evidently retained within this zone. Late stage

Callinectes larvae were most abundant outside the coastal boundary layer in my collections as well as in those of Nichols and Keney (1963). *Callinectes* juveniles or adults were not collected during this study in extensive benthic sampling (otter and small biological trawls, dredge and grab samplers), and small adults were collected only once in plankton samples (*C. similis*, $n = 5$, station C1, neuston, October 1975). Thus, this study presents no evidence for recruitment to inshore and estuarine populations, either by juveniles or megalopae; the evidence, however, does not preclude recruitment from the offshore larval population.

General longshore drift in the Middle Atlantic Bight is southwestward (Iselin 1955; Harrison et al. 1967; Bumpus 1973; and others) and may occur as sporadic events rather than in a continuous sweep (Ruzecki et al. 1976). Reversals of the longshore flow, usually confined to a narrow belt close inshore, may occur from April to September (Bumpus 1969, 1973). A general constraint, however, seems to be placed on larval origins, viz. adult populations are more likely to be replenished by recruitment from larval populations spawned to the north. Given a mean longshore drift of 5 cm/s (Bumpus 1973) and a megalopal duration of 5-67 days (Costlow 1967), a megalopa has a range of 22-290 km; at inshore temperature-salinity ranges (20°-25° C, 30-35‰) a megalopa might be transported 26-56 km.

Callinectes megalopae collected on the outer shelf in the winter and spring, as well as some megalopae found there in the summer and fall, probably have southern origins. Water masses of Gulf Stream origin, as meanders and warm-core eddies, have frequently been observed in the slope-outer shelf regions (Saunders 1971; see Wright 1976 for a review). Although large-scale, long-range transport is not evident, the presence of *Callinectes* and *Portunus* megalopae at station J1 in the winter indicates either transport from the south or, less plausibly, delayed metamorphosis of megalopae from Middle Atlantic Bight populations as a result of low winter temperatures. Based on Costlow's (1967) response surfaces, a megalopa in Gulf Stream waters would have a duration of 7-26 days and a range, at 2 kn, of 600-2,300 km. Thus, some megalopae in the Middle Atlantic Bight may originate from late spawning populations to the south. Metamorphosis would be further delayed by depressed temperatures of shelf and slope waters. The presence of definite southern larval forms (e.g., *Dromidia*) in outer shelf collections supports the hypothesis that at least some of the *Callinectes* and other megalopae were produced by southern crab populations.

The developmental model of *Callinectes*, i.e., larval development in shelf waters and subsequent recruitment to inshore and estuarine adult populations, reflects the evolutionary history of the group. Portunids are "reproductively conservative," migrating to waters of oceanic, or near oceanic, salinities to release larvae (Norse 1977). Williams (1974) described *Callinectes* as "a portunid group evolving at the geographic limits of the family, specializing in occupation of estuaries, ..." In this light, the migratory sequence of larval stages is a response to the problems of an essentially marine group invading the estuaries. Spawning areas (marine) may represent a primitive condition, and the spatial sequence of stages returns larvae to habitats in which the adults are successful. It is, as Williams (1974) described it, a "homeostatic developmental feature in the life histories of the species" that has not been carried to an evolutionary conclusion, that is, retention within the estuary for the entire life history.

It can be argued that such a model of development may in part account for the success and widespread distribution of *Callinectes*. If, as Norse (1977) and others have indicated, recruitment occurs through metamorphosis of megalopae rather than immigration of adults, then such a sequence would allow dispersal into numerous estuaries yet assure genetic continuity over broad areas. Such a role has been suggested by Cole and Morgan (1978). Furthermore, it would seem more likely that this is a primitive mechanism retained, rather than developed, through selection pressures.

The essential features of *Callinectes* development appear to be spawning and hatching in or near the primitive habitat (along the shore) during most of the warmer months, maintenance of a large larval population in the shelf waters (chiefly in the surface layers), recruitment from the larval pool, and exploitation of the estuarine habitat as adults.

There is, however, a paradox in the biogeography of *Callinectes* and the spatial sequence of developmental stages. Given the southern affinities of the genus and general southerly longshore movement of waters along most of the

U.S. Atlantic shelf, the distribution of *Callinectes* is counter to the direction of immediate larval transport. Recruitment to adult populations at the northern limits of *Callinectes* is problematical. Not all larvae can originate from parental stocks to the north. This may indicate that recruitment takes place from megalopal populations closer inshore than those reported in this study and by Nichols and Keney (1963), with the coastal boundary layer possibly retaining larvae. The megalopae collected farther offshore may represent larval wastage to parental populations (but not necessarily to the species).

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AN ANALYSIS OF THE UNITED STATES DEMAND FOR FISH MEAL

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ABSTRACT

As fishery management plans are developed under the Fishery Conservation and Management Act of 1976, economic evaluation of management procedures will be necessary. To adequately address the economics of optimum yield, for instance, research will be required in the traditional economic subjects of demand, production and costs, industrial organization, and international trade. This paper addresses the domestic demand for the primary industrial fishery product—fish meal. In developing the demand model the important points are: 1) choice of empirical variables for inclusion in the model, 2) determination of appropriate functional form of the demand equation, 3) treatment of the "simultaneity bias" problem, and 4) choice between a static (or equilibrium) model and a dynamic model. The paper presents maximum likelihood estimates of both the static and dynamic models. With either model the price elasticity of demand is high when fish meal price is low, and is low when price is high.

Analysis of prices and market demand relationships for fish is of increased importance since the enactment of the U.S. Fishery Conservation and Management Act of 1976 (FCMA[2]). The new law not only establishes a zone of Federal control over fisheries from 3 to 200 mi offshore, but it also establishes national standards for fishery management plans which include economic and social aspects. A key concept is that of "optimum yield"—that rate of annual catch "which will provide the greatest overall benefit to the Nation" (FCMA, Sec. 3(18)). Economic benefits to the nation accrue primarily through the consumption of fishery products which are sold in more-or-less free and competitive markets. Market prices can be expected to vary in response to changes in the annual yields permitted under fishery management plans. These price impacts, along with associated changes in real income, cannot be neglected in the development of appropriate management methods. The demand analysis presented in this paper will assist in the determination of optimum yield for fisheries which contribute to the U.S. fish meal supply.

Fish meal is a primary product of the Atlantic and Gulf of Mexico menhaden fisheries and the California anchovy fishery. It also appears as a byproduct of groundfish and tuna processing. It is used as a high protein supplement most commonly mixed with corn, soybean, or cottonseed meal; meat byproduct meal; and vitamins and minerals for feeding to broilers, layers, and turkeys. According to J. Vondruska,[3] fish meal is also used in feeds for mink and other fur-bearing animals, farmed fish, laboratory animals, livestock, and household pets. About 80% of fish meal consumed in the United States goes into poultry feed. A high level of metabolizable energy and such nutritional elements as riboflavin, pantothenic acid, niacin, choline, and several amino acids are contributed to animal feed by the addition of fish meal (Karrick 1963). Most of these constituents are available in high protein vegetable meals, but fish has a particularly high concentration of the amino acids lysine and methionine.

Because the lysine and methionine are necessary for fast growth in chicks, feed mixers generally seek to include between 2 and 8% fish meal in broiler rations. With >8% fish meal, the poultry tends to pick up a "fishy" flavor. With <2% fish meal, further substitution of vegetable protein meals for fish meal will result in slower growth because the fixed quantity of feed eaten per day per chick cannot contain the ideal mix of amino acids. When fish meal is extremely high priced or

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[2]Public Law 94-265, 94th Congress, 2d Session 13 April 1976, 16 USC 1801 et seq. (Suppl. 1977). Hereafter, FCMA.

[3]J. Vondruska. 1979. Postwar production, consumption, and prices of fish meal. Unpubl. manuscr., 66 p. National Marine Fisheries Service, 3300 Whitehaven St., N.W., Washington, DC 20235.

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unavailable, the lysine and methionine content of the feed can be augmented with synthetic proteins. Kolhonen (1974) described the development of synthetic methionine and lysine for use in feed formulas.

Linear programming has been widely adopted by formula feed manufacturers in the United States and western Europe (Kolhonen 1974). Least-cost combinations of feed constituents needed for adequate nutrition are quickly and accurately computed for any vector of constituent prices. Thus, the demand for feed ingredients is expected to exhibit great sensitivity to relative prices. In a recent examination of demand for agricultural feed ingredients, Meilke (1974) reported that price elasticities are generally >2 in absolute value. It is expected that the demand for fish meal will be elastic also, at least when available quantities allow the feed formula manufacturers to include between 2 and 8% fish meal in poultry rations. When the supply of fish meal is low enough to jeopardize the maintenance of at least 2% fish meal, the demand may become inelastic. Thus, one hypothesis to be tested is that the own price elasticity of demand for fish meal falls with increasing price and decreasing quantity.

Markets for fish meal in the United States are, for obvious reasons, concentrated in the poultry-producing regions—California, Arkansas, and states in the Deep South. Domestic production of fish meal occurs mainly in California, the Gulf Coast States, and the South Atlantic States. In some years, however, much of the domestic supply is imported from major foreign producers such as Peru. Foreign meal is a perfect substitute for the domestic product, but the supply of foreign meal has undergone tremendous fluctuations due to variations in fish stocks (especially the Peruvian anchoveta, *Engraulis ringens*). Domestic supplies have also been strongly influenced by uncontrolled variations in domestic stocks (especially menhaden *Brevoortia tyannus* and *B. patronus*) and by administrative decisions of fishery management agencies (California's anchovy, *Engraulis mordax*, fishery, e.g., see Pacific Fishery Management Council 1978: 31660-31664). On the supply side of the domestic market, therefore, the major fluctuations are not price induced, but are due to exogeneous factors. On the demand side the poultry industry experienced a steady expansion starting in the early 1950's and continuing until about 1970.

DEVELOPMENT OF DEMAND MODEL

Demand and price analysis has been a cornerstone of applied economic research since the 1930's (Working 1927; Schultz 1938; Wold and Juréen 1953). Agricultural economists have been particularly active in developing demand models for commodities. Research on demand for fish is of more recent vintage but differs in few important respects from that for agricultural commodities. For an excellent review of the historical development of demand analysis, see Waugh and Norton (1969). Among the methodological issues addressed in applied demand studies are: 1) specification of the demand model, 2) development of appropriate functional forms, 3) treatment of simultaneity bias in market demand and supply function estimates, and 4) incorporation of dynamic response mechanisms in the demand model. These issues are discussed seriatim.

Specification

The specification of a demand model consists of the choice of dependent and independent variables. Annual quantity demanded, as measured by quantity purchased, should be the dependent variable. Purchased quantities are difficult to obtain, however, while production, import, and export statistics are well documented. Also, meals derived from different sources differ in protein content and sell at different prices. Both the quantities and the prices must be aggregated such that they represent a reasonably homogeneous commodity. Fish meal quantities (Table 1, columns 1-6) are converted to a protein equivalent basis by multiplying the quantity of each type of meal by the prevailing percentage of protein content. The total available domestic quantity, computed by summation of protein equivalent fish meals and subtraction of exports, is listed in Table 1, column 7. Similarly, since the prices of the various fish meal types (Table 2, columns 1-4) are based on protein content, each price is converted to a protein basis. The aggregate price of fish meal introduced as an independent variable in the demand model is the average price per unit protein for all meal supplied to the U.S. market (Table 2, column 5). Some specification error may enter the model because domestic supply rather than quantity purchased is used for the dependent variable, but this problem is unavoidable with available information.

TABLE 1.—United States fish meal supplies, 1955-76 (thousands of metric tons). (National Marine Fisheries Service 1975, 1977.)

Year	(1) Menhaden	(2) Tuna	(3) Anchovy	(4) Other[1]	(5) Imports	(6) Exports	(7) Total supply protein basis[2]
1955	172.9	21.2	0.0	37.6	88.9	n.a.[3]	195.8
1956	191.1	23.9	0.0	44.1	82.0	n.a.	207.5
1957	156.4	23.3	0.0	51.3	73.7	n.a.	185.3
1958	143.4	23.0	0.0	50.2	91.1	n.a.	188.0
1959	203.1	23.0	0.0	43.1	120.6	n.a.	238.8
1960	198.1	24.0	0.0	33.1	119.4	n.a.	229.6
1961	224.6	19.2	0.0	28.8	197.6	n.a.	291.0
1962	217.5	24.1	0.0	31.5	228.9	n.a.	311.4
1963	167.1	24.5	0.0	33.4	341.4	n.a.	355.7
1964	145.4	19.1	0.0	39.6	398.3	n.a.	380.4
1965	159.7	23.0	0.0	37.3	245.5	n.a.	290.4
1966	122.5	23.0	4.1	42.9	406.2	n.a.	378.6
1967	108.1	23.1	5.1	46.5	591.0	n.a.	492.9
1968	129.9	26.1	2.5	47.4	775.9	n.a.	626.7
1969	144.7	24.4	10.3	42.1	325.1	n.a.	343.6
1970	171.1	24.2	14.7	23.2	227.8	4.3	284.9
1971	200.4	26.6	6.9	22.7	256.9	9.2	314.4
1972	175.6	39.2	10.1	23.8	355.6	9.5	373.2
1973	171.3	39.6	20.0	22.4	62.1	33.3	171.4
1974	185.0	43.7	12.8	23.0	62.0	50.3	167.2
1975	173.6	33.7	25.1	20.9	107.4	10.7	215.0
1976	192.9	36.4	19.9	22.0	127.4	30.0	226.7

[1]Primarily from offal, waste, and scrap from groundfish and herring.
[2]Converted to protein as follows: menhaden, exports, and other meal assumed to be 60% protein; anchovy and imports assumed to be 65% protein; tuna meal assumed to be 55% protein. Total supply is production plus imports minus exports.
[3]n.a. means data not available.

TABLE 2.—Annual average prices for various fish meals and average price per unit of protein in fish meal in the United States. (National Marine Fisheries Service 1975.)

Year	(1) Menhaden	(2) Tuna	(3) Domestic anchovy	(4) Peruvian anchovy	(5) Average price per unit protein in fish meal: Actual[1]	(5) Average price per unit protein in fish meal: Deflated[2]
	dollars per metric ton of meal					
1955	123.4	130.7	—	—	1.99	4.34
1956	121.7	121.7	—	—	1.97	4.16
1957	117.7	114.8	—	121.5	1.95	4.01
1958	125.0	124.8	—	128.2	2.01	4.19
1959	116.2	117.1	—	131.9	1.95	3.94
1960	84.4	86.0	—	86.1	1.39	2.80
1961	106.4	99.7	—	100.0	1.69	3.40
1962	112.6	109.5	—	111.2	1.81	3.64
1963	114.1	106.2	—	109.7	1.76	3.58
1964	119.3	115.8	—	119.7	1.88	3.81
1965	152.9	143.2	—	140.3	2.30	4.63
1966	146.1	134.4	137.3	141.9	2.23	4.33
1967	123.8	117.6	117.5	118.1	1.86	3.57
1968	131.8	114.2	110.7	118.8	1.88	3.53
1969	158.1	132.6	137.9	142.5	2.31	4.24
1970	167.4	155.4	156.0	176.4	2.72	4.72
1971	143.3	128.0	140.4	150.7	2.33	3.92
1972	168.3	141.4	154.1	162.6	2.59	4.15
1973	433.8	359.6	365.5	409.8	6.75	9.70
1974	250.5	245.5	270.3	260.6	4.15	4.99
1975	216.9	206.3	214.8	226.5	3.54	3.88
1976	314.3	347.8	247.5	309.9	4.92	5.15

[1]For each meal, price per unit protein equals price per ton divided by percent protein. Average price computed by weighting the price per unit protein for each meal by the proportion of U.S. fish meal protein supplied by that meal.
[2]Deflated by Wholesale Price Index, all commodities (January 1977 = 100).

In addition to the price of fish meal, the demand model should contain independent variables representing 1) the prices of close substitute products, 2) prices of complementary products, and 3) the level of production activity that governs the demand for fish meal. Several high protein meals (e.g., soybean, cottonseed, meat, and bone meals) are potential substitutes for fish meal in poultry rations. Soybean meal is the most common substitute, and its price is used as an independent variable in the demand model. The price of corn meal (Table 3, column 2) is introduced as a complementary product price. Demand for fish meal is expected to increase when the price of a substitute product increases, and is expected to decrease when the price of a complementary product increases. Finally, the overall production of poultry products would cause shifts in the level of demand for fish meal independently of the prices. The poultry and egg production index (Table 3, column 3) is adopted as the appropriate measure of this factor.

In summary, the fish meal demand model is specified as follows:

1) Quantity demanded, the independent variable, is represented by annual production plus net imports of protein-equivalent meal.

2) Annual price of fish meal is measured as the weighted average of the prices per unit protein for all domestically supplied meals.

TABLE 3.—Exogenous variables in the fish meal demand model.

Year	Price of domestic soybean meal[1]	Price of domestic corn[2]	Poultry and egg production index[3] (1976 = 100)
	dollars per metric ton		
1955	51.6	2.24	58
1956	46.5	2.30	63
1957	42.7	2.06	64
1958	50.8	1.99	68
1959	51.3	1.94	70
1960	48.2	1.84	70
1961	57.3	1.80	75
1962	60.3	1.80	75
1963	65.8	2.00	77
1964	62.8	1.99	80
1965	64.9	2.07	83
1966	76.0	2.18	88
1967	69.4	2.06	92
1968	70.3	1.80	90
1969	67.6	1.96	92
1970	71.8	2.19	97
1971	70.7	2.15	98
1972	95.2	2.10	100
1973	216.3	3.57	97
1974	127.8	5.20	97
1975	112.6	4.71	94
1976	147.5	4.37	100

[1]Forty-four percent protein. Simple average price at Decatur, Ill., from National Marine Fisheries Service (1977).
[2]Price of No. 2 yellow corn, Chicago. USDA, ERS, Poultry and Egg Situation, PES-294, 1965-77.
[3]From Schultze et al. (1979).

3) Annual domestic price of corn and annual domestic price of soybean meal are introduced as complementary and substitute product prices.
4) The trend in aggregate demand over time is accounted for by the aggregate poultry and egg production in the United States.

All of the variables expressed in dollars are deflated by the Wholesale Price Index to eliminate spurious correlations caused by the inflationary trend.

Functional Form

Demand studies typically utilize least squares regression methodology with either a linear or a log-linear equation. As noted by Chang (1977), however, there is no a priori reason to choose one of these forms. Each form imposes some fairly strict conditions upon the characteristics of the demand function which may contradict theoretical considerations or actual experience. Linear equations imply that the elasticity of demand with respect to any independent variable is a decreasing function of that variable; a log-linear equation implies constant elasticities. Chang suggests that the income elasticity of demand for meat should fall with rising income. A similar consideration applies to fish meal demand. At low prices, feed manufacturers would use near maximum amounts of fish meal allowable and could easily substitute soybean meal for fish meal. With relatively high fish meal prices, feed manufacturers would use a smaller proportion of fish meal, but as price rises further it would be increasingly difficult to maintain desired quantities of lysine and methionine by substitution of soybean meal. Thus it is clearly unwarranted to rule out increasing price elasticity through a priori choice of functional form.

The function to be fitted by regression analysis can be chosen by determining the appropriate transformation of variables for the linear least squares procedure. The log-linear transformation is a special case of a parametric family of transformations introduced by Box and Cox (1964). The parameter defines the transformation

$$x^* = (x^\lambda - 1)/\lambda. \qquad (1)$$

Equation (1) is linear for $\lambda = 1$, and becomes logarithmic as λ approaches zero. The demand function is expressed as

$$q^* = b_0 + b_1 x_1^* + \ldots + b_k x_k^* + u \qquad (2)$$

where q is the quantity demanded, the x's are the independent variables affecting demand, u_t is a stochastic error term, and the b_i and λ are parameters to be determined. The superscript * indicates that the variable has been transformed as in Equation (1).

Price elasticity of demand is defined as the absolute value of the ratio of percentage change in quantity demanded to percentage change in price. Assuming that the first independent variable is the price, $E = \left|\frac{\partial q}{\partial x}\right| \cdot \left(\frac{x_1}{q}\right)$. From Equation (2) we get

$$E = |b_1|(q/x_1)^{-\lambda}. \qquad (3)$$

The elasticity defined in Equation (3) is an increasing function of x_1 when $\lambda > 0$, and is a decreasing function of x_1 when $\lambda < 0$. Thus the estimate of the transformation parameter λ provides a test of whether the price elasticity increases, decreases, or remains fixed along the demand curve.

Simultaneity Bias

In economic theory, the supply and demand curves interact to determine the market price. Over a period of time, shifts in both supply and demand factors cause the market price and observed quantities of products to vary. Without these shifts, only one price and quantity would be observed, making it impossible to estimate a demand or supply curve. When the demand curve remains stable, the observed price-quantity pairs "trace out" the demand curve with, of course, some stochastic error, and a regression analysis will result in a demand curve estimate. When the supply curve remains stable, the observed data will fall along the supply curve, and a regression analysis of the price-quantity relationship results in a supply curve estimate. If shifts in both demand and supply occur, the resulting data will not unambiguously identify either of these two curves, and an ordinary least squares regression will generally result in a set of parameters reflecting neither the supply curve nor the demand

curve. In this case the estimated parameters are said to suffer from simultaneity bias.

The general statistical problems associated with estimation of individual structural relationships in a simultaneous equation system were first examined by Haavelmo (1943). Development of appropriate statistical methods for estimating simultaneous equation systems has been a major area of research for econometricians over the last two decades (Kmenta 1971). In estimating the demand curve for fish meal, however, direct regression estimates seem appropriate, because most of the observed variations in annual fish meal supplies are due to exogeneous shifts rather than price-induced movements along a stable supply curve. Production of fish meal is subject to wide fluctuations due to uncontrolled variations in the fish stocks exploited (Kolhonen 1974). At the same time, formula feed and poultry industries have remained relatively stable during the last 20 yr except for the secular growth accounted for in the analysis. Under conditions in which the random shifts in supply are much greater than the corresponding shifts in demand, the ordinary least squares procedure results in no significant simultaneity bias (Rao and Miller 1971).

Lagged Response Mechanisms

The use of annual price and quantity data for estimating the demand function requires that the response to a change in price occurs rather rapidly, at least within a period of time much shorter than a year. Since most domestic formula feed manufacturers employ professional nutritionists and cost-minimizing computer routines in calculating formulas, the response to changes in the vector of prices is probably rapid. If so, each annual quantity consumed may be assumed to represent at least approximately an equilibrium demand response to the set of independent variables. The assumption of rapid response and equilibrium approximation, however, has not been directly verified. In the interests of rigor it is useful, therefore, to consider alternative assumptions.

A lagged response to a change in price may occur due to rigidities in mixing procedures or personnel, inventory management problems, or time lags in renegotiating contracts for supply of input or sales of products. If any of these factors results in a sluggish response in the substitution between fish meal and other protein meals, the effect of a price change may be drawn out over several periods of time. A fairly simple model for representing a lagged response is the "partial adjustment model" originally developed by Nerlove (1958). Corresponding to any given level of the independent variable, p, there is an optimal or desired level of the dependent variable q. For a demand function with one independent variable, the level of demand fully adjusted to input prices by formula manufacturers represents the desired level of fish meal usage:

$$q_t^d = b\,p_t + u_t \tag{4}$$

where the superscript d signifies desired level.

Because purchasers of meal cannot immediately adjust to this desired level of usage, the demand Equation (4) is not directly observable. By assuming a simple structure to the adjustment process, however, an estimable equation is obtained. The partial model assumes that a fixed percentage of the adjustment to desired level is made each year. This introduces the difference equation

$$q_t - q_{t-1} = \gamma(q_t^d - q_{t-1}). \tag{5}$$

Solving this for q_t and substituting from Equation (4) yields

$$q_t = b\,\gamma\,p_t + (1-\gamma)q_{t-1} + \gamma u_t. \tag{6}$$

The adjustment parameter, γ, must be a positive number ≤ 1. Larger values of γ imply more rapid adjustment to changes in the independent variable. The impact of a unit change in p_t is distributed over time in an exponentially decaying fashion with successive annual changes in q being equal to $b\gamma$, $b\gamma(1-\gamma)$, $b\gamma(1-\gamma)^2$, and so forth. The ultimate change in q due to a change in p is

$$\Delta q = b\Delta p \sum_{j=0}^{\infty} \gamma(1-\gamma)^j = b\Delta p \tag{7}$$

where j = lag. The elements in the sequence under the summation sign are all positive fractions, and sum to one, so that the sequence can be treated like a probability distribution. Each element represents the percentage of the total effect occuring in year t, and the mean of the distribution, $(1-\gamma)/\gamma$, represents the mean lag in the adjustment process. Distributed lag models like that in Equation (4) result from other conceptual models such as models of expectations formation

or habit formation. And the exponentially distributed lag is but one of a large class of more complex lag models (Griliches 1967; Kmenta 1971; Rao and Miller 1971).

Application of the partial adjustment model to the demand Equation (2) results in the following:

$$q^*_t = a_0 + \sum_{i=1}^{4} a_i x^*_i + a_5 q^*_{t-1} + u_t \qquad (8)$$

where the coefficients a_i can be interpreted in terms of the coefficients of Equation (2) as follows:

$$a_0 = \gamma b_0$$
$$a_i = \gamma b_i; i = 1, \ldots 4$$
$$a_5 = (1 - \gamma).$$

STATISTICAL PROCEDURES

For a given value of the transformation parameter, λ, the coefficients of either the equilibrium model [Equation (2)] or the partial Adjustment model [Equation (8)] can be estimated by the ordinary least squares method. Two statistical issues requiring further development, however, are the selection of the "best" value for λ, and the test for significance of the lagged adjustment parameter. An appropriate procedure for estimation of λ was first suggested by Box and Cox (1964). The procedure is more clearly explained in the linear regression context by Kmenta (1971) and is reviewed by Chang (1977). For a fixed value of λ, the linear regression procedure yields an estimate of the error variance $\hat{\sigma}^2$. Box and Cox showed that the maximized log likelihood is, except for a constant,

$$L_{\max}(\lambda) = -(N/2) \log \hat{\sigma}^2(\lambda) + (\lambda - 1)\Sigma \log q_i. \qquad (9)$$

A maximum likelihood estimate of λ can, therefore, be found by searching through successive values of λ to maximize Equation (9). The use of this likelihood function implies, of course, that the error terms conform to full normal theory assumptions, i.e., that the u_t are independently normally distributed with zero mean and constant variance. An approximate 100% $(1 - \alpha)$ confidence region for λ is defined by

$$L_{\max}(\hat{\lambda}) - L_{\max}(\lambda) < \tfrac{1}{2}\, \chi_1^2(\alpha) \qquad (10)$$

where $\chi_1^2(\alpha)$ represents the value of the chi-square distribution with 1 df (Box and Cox 1964).

Serial correlation in the errors of the regression model raises problems in the interpretation of the test statistics for the nonlagged variables and the lagged adjustment parameter, and contradicts the assumptions of the log likelihood function. Careful examination of the hypotheses and statistics regarding the residuals of the regression equation is clearly necessary. Existence of serial correlation in the errors of the static demand model can be tested with the Durbin-Watson statistic. If no serial correlation is apparent in the residuals, then neither the distributed lag model nor the serial correlation model need be considered. If serial correlation is present in the residuals of the static model, then the problem is to distinguish between the distributed lag model and the serial correlation model.

Griliches (1967) showed that the serial correlation and lagged adjustment models cannot be distinguished by a simple t-test on the adjustment parameter. For example, if errors generated by a first order Markov process, i.e., $e_t = se_{t-1} + u_t$, occur in a regression equation, the coefficients of the lagged variables may be judged significant by the usual t-test even though there is no real lagged response in the underlying structural relationship. Similarly, it can be shown that serially correlated residuals will occur if a nonlagged model is mistakenly fit to data from an inherently dynamic process.

Although there is no fully satisfactory method for determining which model is the truth, Griliches (1967) developed a provisional test. Briefly, the serial correlation model is

$$q_t = a_0 + \sum_i a_i x_{it} + e_t \qquad (11a)$$

$$e_t = se_{t-1} + u_t \qquad (11b)$$

where s is a positive fraction and u_t is a nonserially correlated error term. From Equation (11a), $e_{t-1} = q_{t-1} - a_0 - \Sigma_i a_i x_{it-1}$; so that $e_t = s(q_{t-1} - a_0 - \Sigma_i a_i x_{it-1}) + u_t$. Substituting this into Equation (11a) yields

$$q_t = (1 - s)a_0 + \sum_i (a_i x_{it} - b_i x_{it-1}) + s\, q_{t-1} + u_t. \qquad (12)$$

When Equation (12) is computed, the serial correlation model implies that $a_i s = -b_i$ for each i. Griliches suggested that the first-order serial correlation model be rejected if these four equalities do not appear to hold. Thus, there are four hypotheses of the following form:

$$H_0: (b_i + sa_i) = 0. \quad (13)$$

An approximate sample variance for $(b_i + sa_i)$ is computed by the "delta method" described by Seber (1973). The expression for approximate variance of a function of a vector of random variables, $G(x)$, is

$$v[G(x)] = \Sigma v(x_i)\left(\frac{\partial G}{\partial x_i}\right)^2 + 2\sum_{i<j}\sum \operatorname{cov}(x_i x_j)\left(\frac{\partial G}{\partial x_i}\right)\left(\frac{\partial G}{\partial x_j}\right). \quad (14)$$

Assuming that the estimate of $(b_i + sa_i)$ from the regression equation is approximately normally distributed, the following ratio will be approximately distributed as an F-statistic with 1 and $(n - r)$ df (where r is the number of regression parameters estimated):

$$(b_i + sa_i)^2/v[b_i + sa_i] \approx F(1, n - r). \quad (15)$$

Since the serial correlation model requires each of the four hypotheses to hold, a definite rejection of one or more of the hypotheses may be taken as evidence against the serial correlation model and in support of the partial adjustment model. Because of the lack of rigor in the suggested testing procedure, however, caution must be exercised in drawing conclusions.

RESULTS

Ordinary least squares estimates of the static demand Equation (2) were computed for a range of values for the transformation parameter λ. The regression coefficients and statistics of most interest are listed in Table 4. A value of $\lambda = -0.55$ maximizes the log likelihood function, but the 95% confidence interval for λ is 0.2 to −1.4. The interval includes the logarithmic transformation ($\lambda = 0$), but not the linear transformation ($\lambda = 1$). The negative value of λ, which implies a price elasticity of demand that decreases as quantity decreases, conforms to expectations. The signs of all the coefficients are also consistent with prior expectations; demand is diminished by increasing price of fish meal or corn meal, and is increased by increasing price of soybean meal and by expanding poultry and egg production. Application of t-tests to the coefficients of the equation with $\lambda = -0.55$ indicates statistical significance with 99% confidence for the coefficients of fish meal price and corn meal price, and with 90% confidence for the coefficient of soybean meal price. The poultry and egg production index appears to be an insignificant influence on fish meal demand by the t-test. But this is insufficient reason for eliminating a theoretically important variable from the equation.

The squared multiple correlation coefficient, $r^2 = 0.73$, indicates a reasonably "good fit" for a demand equation estimate from time-series data.

TABLE 4.—Regressions for determining maximum log-likelihood of static demand function. P_f = price of fish meal, P_s = price of soybean meal, P_c = price of corn feed, Q_p = poultry and egg production index. Superscript * indicates Box-Cox transformation expressed in Equation (1).

Transformation parameter (λ)	Intercept	Coefficient P_f^*	P_s^*	P_c^*	Q_p^*	R^2	D-W[1]	$L\max(\lambda)$
0.5	44.184	−10.144	9.588	−8.597	0.816	0.695	0.754	−91.21
[2]0.2	12.499	−2.620	2.174	−2.532	0.545	0.714	0.716	−89.70
0.0	6.054	−1.064	0.812	−1.125	0.413	0.722	0.704	−88.97
−0.20	3.324	−0.432	0.305	−0.501	0.311	0.727	0.705	−88.48
−0.50	1.731	−0.112	0.071	−0.150	0.199	0.730	0.725	−88.14
[3]−0.55	1.592	−0.089	0.056	−0.123	0.184	0.730	0.731	−88.13
	(5.108)	(−2.602)	(1.864)	(−3.489)	(0.976)			
−0.60	1.474	−0.071	0.044	−0.100	0.171	0.730	0.735	−88.14
−0.70	1.282	−0.455	0.027	−0.067	0.146	0.729	0.751	−88.18
−1.0	0.929	−0.012	0.007	−0.020	0.088	0.724	0.801	−88.56
−1.2	0.789	−0.005	0.003	−0.009	0.061	0.719	0.839	−89.02
[2]−1.4	0.687	−0.002	0.001	−0.004	0.042	0.711	0.879	−89.61

[1]D-W stands for Durbin-Watson statistic.
[2]Indicates approximate 90% confidence interval for λ.
[3]Indicates maximum likelihood estimate (t-values in parenthesis).

The Durbin-Watson statistic (0.731) is below the lower critical value (d_l = 0.86 for 21 observations and 4 parameter estimates), indicating significant serial correlation in the errors of the demand model. As suggested above, this serial correlation may be caused by incorrect specification of a static model when a dynamic adjustment model would be more appropriate, or it may reflect true serial correlation in the errors which may in turn be due to some other source of misspecification.

Following the suggestion by Griliches (1967), a regression equation with lagged dependent and independent variables was computed (Table 5). The F-statistics for the four hypotheses associated with the serial correlation model range from 0.119 to 6.516. The critical value for each hypothesis (with $P<0.05$ and for 1 and 11 df) is 4.84. Clearly, only one of the four hypotheses, the one associated with the soybean price, can be rejected with great confidence. Even this may be misleading, because the probability of wrongly rejecting at least one of four hypotheses at the 5% level is 0.183[4]. Due to the provisional nature of the test procedure and the inconclusiveness of the result, it is useful to consider both the static and distributed lag models as plausible representations.

The distributed lag model [Equation (8)] was estimated by ordinary least squares for several values of the transformation parameter λ. Regression coefficients and pertinent statistics for the distributed lag model are listed in Table 6. The log-likelihood function is greatest for λ = −0.3, and the approximate 95% confidence interval for λ is −1.0 to 0.22. As in the earlier nonlagged model, the coefficients of the independent variables have the appropriate signs. Since the coefficient of the lagged dependent variable can be interpreted via Equation (5) as one minus the rate of adjustment parameter, the partial adjustment parameter is 0.503. This implies an average lag of slightly less than one. As expected, buyers of fish meal generally adjust to changing conditions and prices within a year.

TABLE 5.—Estimates for demand function parameters with all variables lagged.[1] Transformation parameter, λ, equals −0.55; and all symbols are as explained in Table 4. R^2 = 0.855.

Variable	Estimated coefficient	SE	F-statistic[2]
$P_f^*(t)$	−0.07521	0.03208	0.455
$P_f^*(t-1)$	0.01861	0.03258	
$P_s^*(t)$	0.07498	0.0297	6.516
$P_s^*(t-1)$	0.03765	0.03609	
$P_c^*(t)$	−0.2059	0.07897	0.119
$P_c^*(t-1)$	0.1159	0.04239	
$Q_p^*(t)$	1.3352	0.5497	4.006
$Q_p^*(t-1)$	−1.5422	0.5309	
$q^*(t-1)$	0.5164	0.1979	—

[1] $q^*(t) = a_0 + a_1P_f^*(t) + b_1P_f^*(t-1) + a_2P_s^*(t) + b_2P_s^*(t-1) + a_3P_c^*(t) + b_3P_c^*(t-1) + a_4Q_p^*(t) + b_4Q_p^*(t-1) + a_5q^*(t-1)$.

[2] The hypothesis to be tested is $(b_i + a_i\,a_5) = 0$; and the corresponding F-statistic is $F_i = (b_i + a_i\,a_5)^2/\mathrm{Var}(b_i + a_i\,a_5)$.

DISCUSSION

Both the static demand model and the partial adjustment model provide reasonable levels of statistical fit to the historical data series and the signs and magnitudes of the regression

[4] The probability of type 1 error in a single test is 0.05. If four tests are made the probability of making at least one type 1 error is one minus the probability of making no type 1 errors, i.e., $1 - (0.95)^4$.

TABLE 6.—Regression equations for determining maximum log-likelihood of distributed lag form of demand function. P_f = price of fish meal, P_s = price of soybean meal, P_c = price of corn feed, Q_p = poultry and egg production index, q_{t-1} = quantity of fish meal, lagged. Superscript * indicates Box-Cox transformation expressed in Equation (1).

Transformation parameter (λ)	Intercept	Coefficient P_f^*	P_s^*	P_c^*	Q_p^*	q_{t-1}^*	R^2	$L\max(\lambda)$
1.0	297.904	−103.141	105.367	−21.018	0.694	0.468	0.766	−81.133
0.6	40.639	−16.897	13.097	−3.821	0.537	0.485	0.800	−83.953
0.1	4.122	−1.792	0.902	−0.482	0.389	0.498	0.822	−81.507
0	2.761	−1.147	0.522	−0.323	0.363	0.499	0.824	−81.259
−0.2	1.373	−0.470	0.170	−0.147	0.314	0.498	0.825	−81.014
[1]−0.3	1.030	−0.301	0.098	−0.100	0.291	0.497	0.824	−81.013
	(1.396)	(−3.567)	(1.161)	(−0.840)	(1.189)	(2.907)		
−0.4	0.809	−0.193	0.056	−0.068	0.268	0.494	0.822	−81.090
−0.5	0.665	−0.124	0.031	−0.047	0.247	0.491	0.819	−81.239
−1.0	0.404	−0.013	0.002	−0.008	0.153	0.458	0.795	−82.853

[1] Indicates maximum likelihood estimate (t-values in parentheses).

coefficients satisfy prior expectations. Because it yields a significantly higher r^2, and because the test for serial correlation suggested by Griliches (1967) lends it support, I tend to favor the distributed lag model. But the evidence is not really conclusive. For one thing, the "Griliches test" looks only for first-order serial correlation, and it will probably fail to give correct guidance when more complex residual generating processes are present. Another difficulty is the lower precision of the regression coefficients in the distributed lag model. The importance of this depends upon how the demand function is to be used. In fisheries management applications the most important use of the demand model will be for predicting price effects resulting from changes in annual production.

To compare the two demand models, the equations are transformed to give quantity demanded in natural units (tons of fish meal proteins) and the 1976 values of independent variables other than fish meal price are inserted. The resulting relationships between price and quantity are

$$q_t = \left[-0.00389 + 0.04916\left(\frac{P_f^{-0.55} - 1}{-0.55}\right)\right]^{\frac{1}{-0.55}} \qquad (16)$$

for the static demand model, and

$$q_t = \left[-0.03486 + 0.18001\left(\frac{P_f^{-0.3} - 1}{-0.3}\right)\right]^{\frac{1}{-0.3}} \qquad (17)$$

TABLE 7.—Demand predictions ($\hat{q}$) and price elasticities (E) for static demand ($\lambda = -0.55$) and partial adjustment ($\lambda = -0.3$) models.

Price of fish meal protein (P_f)	Static demand model		Partial adjustment model	
	$\hat{q}$	E	$\hat{q}$	E
2	852.5	2.49	4,971.0	6.26
4	295.2	0.95	372.3	2.34
6	215.1	0.64	168.8	1.63
8	182.8	0.50	110.7	1.32
10	165.0	0.42	84.2	1.14

for the dynamic demand model. Quantities predicted by Equations (15) and (16) and price elasticities of demand for a range of prices are listed in Table 7. From the Table and Figure 1 it is clear that the two demand models are grossly similar. At low supply levels (less than about 250 t), however, the predicted price responses are greatly different, as are the quantities demanded when prices are low (<$4 per unit protein). Thus, any conclusions reached on the basis of this demand analysis will be sensitive to the specification of the demand function.

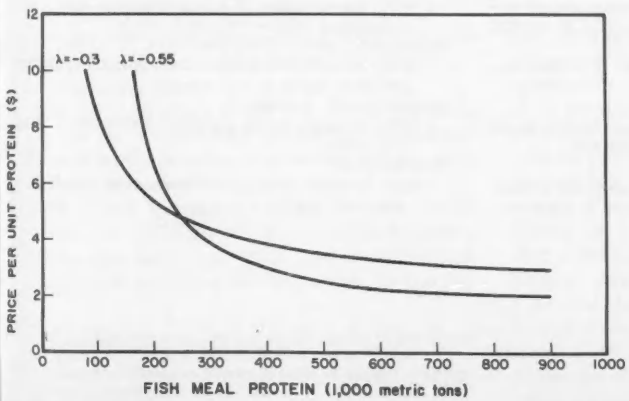

FIGURE 1.—Fish meal demand curves based upon the maximum likelihood estimates of the static demand model ($\lambda = -0.55$) and the partial adjustment model ($\lambda = -0.3$).

Most economic models of fishery management have ignored the influence of landings on the price of fish or fishery products. The assumption of fixed price is a particularly attractive one, because with fixed prices the harvest quantity is proportional to the total revenue. Only the relationship between costs and landings must be added to the model in order to derive economic critertia for optimization. When management programs control landings which are large relative to the market demand, however, the price is likely to become a variable rather than a fixed parameter. The use of demand relationships, such as the one estimated above, will undoubtedly become important as more control is exercised over more fisheries in the United States. The means for incorporating demand analysis into fishery management models is explained by Anderson (1973) and Clark (1976, chapter 5). More extensive use of these complex models which include variable prices will proceed only as fast as the development of solid, empirical demand studies.

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DEVELOPMENT AND STRUCTURE OF FINS AND FIN SUPPORTS IN DOLPHIN FISHES *CORYPHAENA HIPPURUS* AND *CORYPHAENA EQUISELIS* (CORYPHAENIDAE)[1]

THOMAS POTTHOFF[2]

ABSTRACT

The development and structure of the fins and fin supports were studied from a cleared and stained size series of about 400 *Coryphaena hippurus* and about 400 *C. equiselis*. *Coryphaena hippurus* and *C. equiselis* differ in all aspects of fin ray and fin support development; *C. equiselis* is always more advanced than equal-sized *C. hippurus* during development. The species differ in number of fin rays in the single dorsal fin. The pterygiophores of the single dorsal fin each develop from a single cartilage in both species. The cartilage then ossifies to proximal and distal radials. Each fin ray is serially associated with a distal and proximal radial, and each ray is secondarily associated with the following (posterior) proximal radial. Exceptions were found at the anteriormost and posteriormost parts of the dorsal fin. The two species differ only slightly in anal fin ray counts. The pterygiophores of the anal fin are similar in development and structure to those of the dorsal fin. The species do not differ in caudal fin ray counts. The caudal fin rays are supported by some of the bones of the caudal complex, which contains one neural spine, one specialized neural arch, two autogenous haemal spines, one autogenous parhypural bone, five autogenous hypural bones, two paired uroneural bones, and two epural bones. During development, hypurals one and two and hypurals three and four fuse, forming the dorsal and ventral hypural plates. The two epurals fuse into one and the two pairs of uroneurals form one pair. Both species have the same number of pectoral fin rays. In both species, pectoral fin rays are directly supported by the scapula and four radials, and indirectly by the cleithrum and the coracoid. The pectoral suspensorium, which consists of seven bones, connects the pectoral bones to the skull. The posterior process of the coracoid develops as a prominent larval structure that disappears during development. The pelvic fins of both species have one spinous and five soft rays. These fin rays are supported on each side by the pelvic basipterygium. The basipterygium develops in similar fashion to a pterygiophore.

The development and anatomy of the fins and fin supports for *Coryphaena hippurus* and *C. equiselis* have not been described. The purpose of this study was to document the development and anatomy of the fins and fin supports for the family Coryphaenidae and to point up differences in meristic counts and arrangement of fin rays and supporting bones between the two species of *Coryphaena* using cleared and stained material.

No complete study of the fins and fin supports for the two *Coryphaena* species has been done. Studies on the osteology and meristic counts exist without use of cleared and stained material. Jordan and Evermann (1896), Nichols (1909), Gibbs and Collette (1959), Rothschild (1964), Miller and Jorgenson (1973), and Shcherbachev (1973) have published meristic counts for the two species. Clothier (1950) gave the meristic counts and an illustration of the head and the vertebral column for *C. hippurus*. Potthoff (1971), using cleared and stained material, studied meristic counts of *C. equiselis*. Collette et al. (1969) reported the vertebral numbers of the two species, and Gregory (1933) depicted the skull of *C. hippurus* and commented on the phylogenetic relationship of *C. hippurus*. Starks' (1930) description of the pectoral girdle of *C. hippurus* was presented without illustrations.

Many publications deal with the biology (age, growth, reproduction, food) of *Coryphaena* spp., usually *C. hippurus* (Schuck 1951; Williams and Newell 1957; Gibbs and Collette 1959; Kojima 1961, 1963a, b, 1964; Beardsley 1967; Rose and Hassler 1968, 1974; Shcherbachev 1973; Takahashi and Mori 1973). Others document the distribution of *Coryphaena* spp., most often that of *C. hippurus* (Williams 1953; Morrow 1954; Pew 1957; Gibbs and Collette 1959; Kojima 1960, 1964; Tibbo 1962; Shcherbachev 1973; Takahashi and Mori

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1973). Mito (1960) described the eggs and hatched larvae of *C. hippurus*, and Gibbs and Collette (1959) described large larvae and juveniles of both *Coryphaena* species. Hassler and Rainville[3] described the rearing techniques for *C. hippurus* from planktonic eggs and the subsequent growth to juveniles. Burnett-Herkes (1974) worked on *C. hippurus* parasites of the gills and mouth.

METHODS

Size series of 400 specimens of each species were cleared and stained by the enzyme method of Taylor (1967). The bones of four adult specimens (two *C. hippurus* and two *C. equiselis*) were prepared by boiling in water and removing the boiled flesh. Almost all specimens had been caught in the west Atlantic, Gulf of Mexico, and the Caribbean. A few specimens were from the mid-Atlantic, the east Atlantic, and the east Pacific.

For each fin and fin support system, a representative size series was chosen for each species from the cleared and stained material (Table 1). Thus, the same specimen did not necessarily contribute to each of the series.

The terms preflexion, flexion, and postflexion refer to the flexion state of the notochord in the caudal region during larval development. They are used to describe and highlight larval stages based on Ahlstrom et al. (1976).

Only cleared and stained specimens were measured. Preserved larvae were usually too distorted for accurate measurements, but were easily straightened and measured after clearing and staining. Measurements were to the nearest 0.1 of a millimeter using a calibrated ocular micrometer for the smaller specimens (< 20 mm SL) and dial calipers for the larger ones. Each measurement was either notochord length (NL, from the anterior tip of the upper jaw to the posteriormost tip of the notochord) for preflexion and early flexion larvae, or standard length (SL, from the anterior tip of the upper jaw to the posteriormost edge of the hypural bones) for late flexion and postflexion larvae, juveniles, and adults.

All specimens were examined in 100% glycerin under a binocular microscope, and illustrations were drawn with the help of a camera lucida. Ossification was determined from the uptake of alizarin. Very light uptake (pink) of alizarin in a structure was considered as onset of ossification. Cartilage was determined by the presence of structure but absence of red stain, and viewed by carefully manipulating the illumination with the substage mirror. Specimens from which organic calcium had leached due to acid Formalin[4] did not stain and were not used.

The caudal complex terminologies follow Gosline (1961a, b), Nybelin (1963), and Monod (1968).

Counts of pterygiophores and fin rays include very small and vestigial structures such as fin rays that consisted only of a left or right half, or of two pieces not joined at the center.

[3]Hassler, W. W., and R. P. Rainville. 1975. Techniques for hatching and rearing dolphin, *Coryphaena hippurus*, through larvae and juvenile stages. Univ. N.C., Sea Grant Program UNC-SG-75-31, 17 p.

TABLE 1.—Number and length range (in millimeters NL or SL) of cleared and stained specimens of *Coryphaena* spp. used for study of individual fins and their support structures.

Item	*C. hippurus*		*C. equiselis*	
	No.	Length	No.	Length
Dorsal fin	211	5.0-172	161	6.5-230
Pterygiophores	216	5.0-176	197	6.5-230, 314
Anal fin	212	5.0-172	157	6.5-230
Pterygiophores	216	5.0-176	197	6.5-230, 314
Caudal fin	201	5.0-172	138	6.5-230
Caudal complex	47	5.0-172, 690	45	6.5-230, 330
Pectoral fin and supports	123	5.0-172	164	6.5-230
Pelvic fin and supports	105	6.0-176, 449, 920	76	7.0-172, 315, 330

RESULTS

Vertebral Column

The development and structure of the vertebral column was not examined in this study. However, it was noted that development is similar in all respects for the two *Coryphaena* species as it was reported for *Thunnus atlanticus* (Potthoff 1975).

Neural and haemal spines developed from cartilage before pterygiophores, but were difficult to count accurately. In small specimens (5.9-6.3 mm NL) interneural and interhaemal space numbers were estimated from myomere counts.

Dorsal Fin

The fully developed dorsal fin of *C. hippurus* has 58-66 rays (N = 99, $\bar{x}$ = 61.3, SE = 0.17, 24-172 mm SL) and that of *C. equiselis* 52-59 rays (N = 113, $\bar{x}$ = 55.0, SE = 0.15, 18-230 mm SL). Adult counts for *C. hippurus* are obtained be-

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

tween 18 and 24 mm SL and for *C. equiselis* between 13 and 18 mm SL (Figure 1). Gibbs and Collette (1959) reported 46-65 ($\bar{x}$ = 58.4) dorsal fin rays for *C. hippurus* and 48-60 ($\bar{x}$ = 52.6) for *C. equiselis*. My counts and those of Gibbs and Collette (1959) differ because Gibbs and Collette included counts of small specimens (from about 12 mm SL) of both species in their sample and because *C. equiselis* develops a full complement of dorsal fin rays at a smaller size than *C. hippurus* (13-17 mm SL vs. 18-23 mm SL); therefore, more *C. hippurus* than *C. equiselis* with incomplete dorsal fins were counted by Gibbs and Collette, and inclusion of incomplete dorsal fin ray counts widened the range of counts and lowered the mean number of dorsal fin rays. Dorsal fin ray counts reported by Shcherbachev (1973) (46-67 for *C. hippurus* and 48-60 for *C. equiselis*) are from his own data and those of Gibbs and Collette. Rothschild (1964) reported 54-58 ($\bar{x}$ = 57.9) for adult *C. equiselis*, all from the Pacific Ocean. Here, count differences probably resulted from the method of counting (cleared and stained vs. preserved material) but may also have been due to population differences.

Dorsal fin rays were first seen in *C. hippurus* at 6 mm SL and were present in all specimens at 8 mm SL (Figure 1). The smallest specimen of *C. equiselis* (6.5 mm SL) already had 12 dorsal fin rays. Development of the dorsal fin rays for both species started in the dorsal finfold at the posterior third of the body (Figure 2). This was above the 22d-24th myomere for three *C. hippurus* with only 3 or 4 dorsal fin rays. With growth, addition of dorsal fin rays was in an anterior and posterior direction for both species, but more fin rays were added anteriorly (Figure 2). The dorsal fin, despite the more rapid addition of rays anteriorly, reached completion posteriorly at a smaller size of the larvae than anteriorly. This is because more

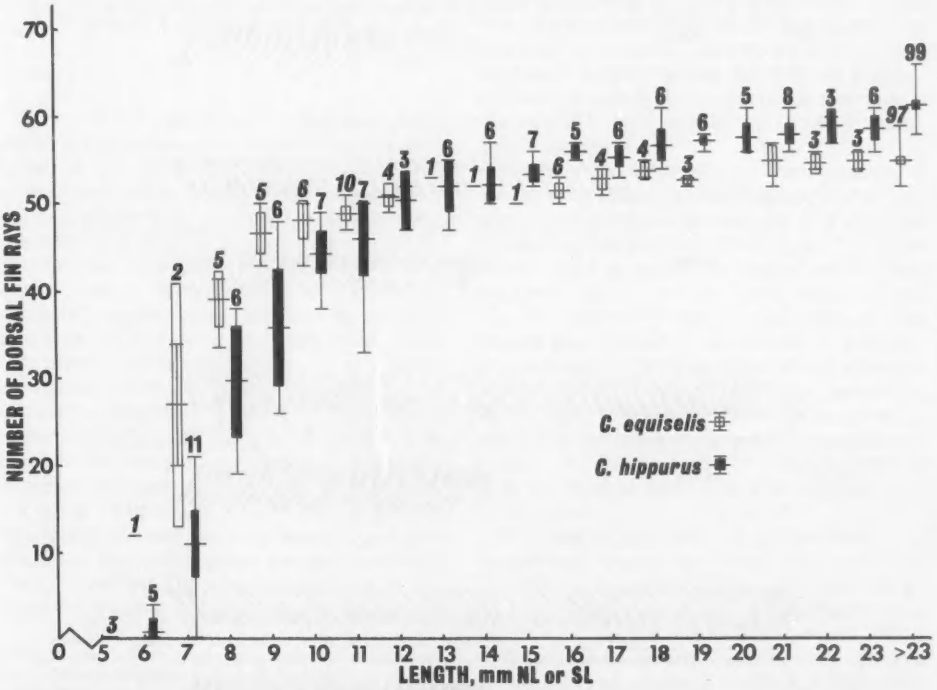
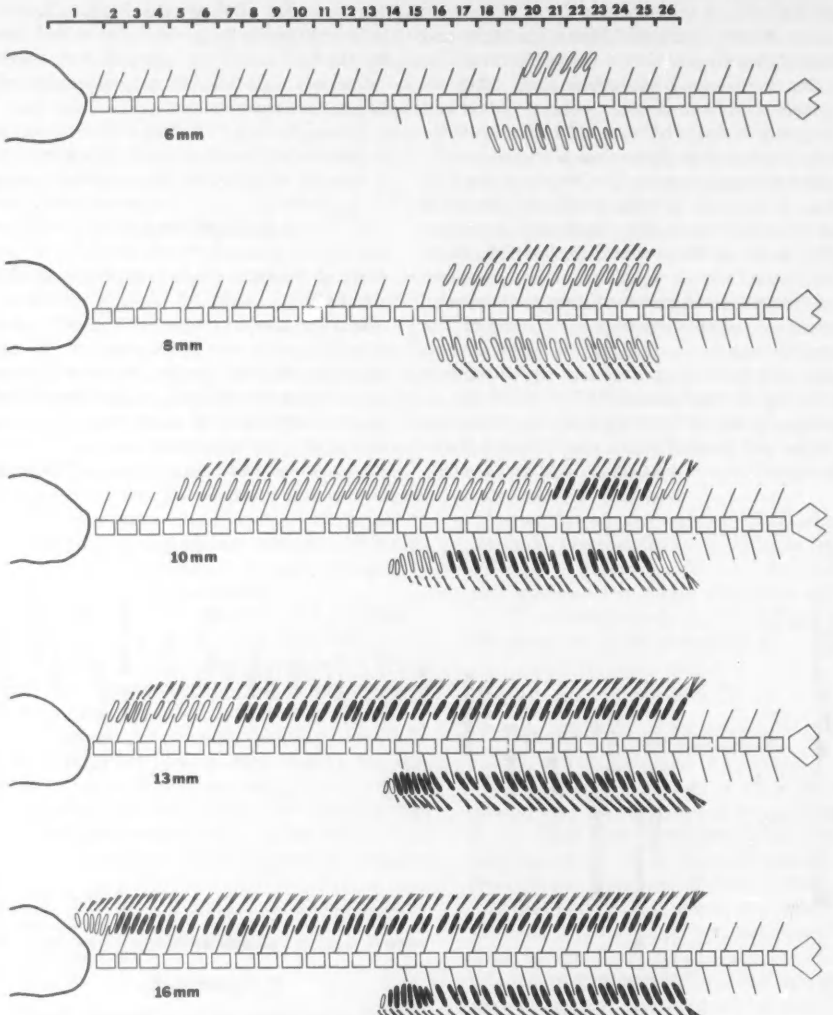


FIGURE 1.—Number of dorsal fin rays in relation to length in 161 *Coryphaena equiselis* (6.5-230 mm NL or SL) and 211 *C. hippurus* (5.0-172 mm NL or SL). Range (vertical line), mean (horizontal line), and 2 standard errors about the mean (white and black bars) are indicated. Number of specimens for each length interval is given above the range and is in italics for *C. equiselis*.


1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26
6 mm
8 mm
10 mm
13 mm
16 mm
36 mm
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26

pterygiophores had to be added from place of origin anteriorly than posteriorly. Small *C. hippurus* (5 mm NL-11 mm SL) usually had fewer fin rays compared to equal-sized *C. equiselis* (Figure 1). Between 12 and 14 mm SL both species had about equal dorsal fin ray numbers. Specimens of *C. hippurus* 15 mm SL and longer usually had more dorsal fin rays than equal-sized *C. equiselis*.

The developmental sequence of dorsal fin rays in *Coryphaena* spp. is similar to that observed in *Trachurus symmetricus* (Ahlstrom and Ball 1954), *Haemulon plumieri* (Saksena and Richards 1975), and *Archosargus rhomboidalis* (Houde and Potthoff 1976). It is as though *Coryphaena* spp. is developing two dorsal fins in the same pattern of the above examples, e.g., first the second dorsal fin followed by the first dorsal. It is of interest to note that most scombroids do not follow this pattern and develop the first dorsal fin first (Voss 1954; Potthoff 1975).

Dorsal Fin Pterygiophores

Counts

There was a supporting pterygiophore in both species of *Coryphaena* in a jointed series for each dorsal fin ray, except for the first two or three anteriormost rays. Each pterygiophore had a proximal and a distal radial. The distal radial was located between the bifurcate base of the fin ray. Proximal and distal radial and fin ray formed a series, hence, a serial association. Each fin ray also closely approximated the following posterior pterygiophore in a secondary association. Thus, each pterygiophore supported a ray in a serial association and an immediately anterior ray in a secondary association. The exceptions were found at the beginning and the end of the fin. The anteriormost pterygiophore supported from one to three rays, but most often two rays (Table 2). Also, in 2 out of 70 specimens of both species, no rays were associated with the anteriormost pterygiophore, and the pterygiophore was very small and almost a vestige. The posteriormost ray in the dorsal fin was a double ray which was serially associated with the posteriormost pterygiophore. This was the only ray in the dorsal fin which lacked a secondary association. Total dorsal fin ray count in both species was either one less than the pterygiophore count, equal to the pterygiophore count, or one or two greater than the pterygiophore count. Thus, the two species differed in their pterygiophore number as they differed in their fin ray counts.

TABLE 2.—Number (adult count) of anteriormost dorsal fin rays without distal radials and number of dorsal fin rays associated with the anteriormost dorsal fin pterygiophore for 28 *Coryphaena hippurus* (78.8-176 mm SL) and 35 *C. equiselis* (74.1-172, 314 mm SL).

Item	Species	Number of anteriormost dorsal fin rays 0	1	2	3
Without distal radials	*C. hippurus*		12	12	4
	C. equiselis	1	6	25	4
Associated with the anteriormost pterygiophore	*C. hippurus*		3	24	1
	C. equiselis		1	17	19

In larvae, juveniles and small-sized adults of *Coryphaena* spp. the proximal radials of the dorsal fin were inserted in interneural spaces. The first interneural space was bounded anteriorly by the head and posteriorly by the first neural spine, followed posteriorly by the remaining interneural spaces which were bounded by all other neural spines (Figure 3).

Fully developed specimens of the two species of *Coryphaena* differed by the number of pterygiophores that occupied the interneural spaces. The number of pterygiophores found in the first interneural space separated the species most of the time, with 10-14 ($\bar{x}$ = 11.0) for *C. hippurus* and 7-11 ($\bar{x}$ = 8.0) for *C. equiselis* (Figures 3, 4). The species also differed in the number of pterygiophores associated with the remainder of the interneural spaces. Although individual variability within each interneural space was too great to allow this character to be used to separate the species, the mean number of pterygiophores in each interneural space was always greater for *C. hippurus*.

The species also differed in the number of interneural spaces that were occupied by the dorsal fin pterygiophores (Figure 3; Tables 3, 4). In *C. hippurus* the dorsal fin pterygiophores extended to the 26th interneural space and seldom to the 27th, whereas in *C. equiselis* they extended to the 28th and seldom to the 27th or 29th space. There was some overlap for the two species in this character, but if the termination of the anal fin pterygiophores was taken into account, together

FIGURE 2.—Schematic representation of dorsal and anal fin and pterygiophore development in *Coryphaena hippurus* in relation to the vertebral column and head. Oval-shaped representation of pterygiophores are cartilaginous when white and ossifying when black. Scale represents interneural and interhaemal spaces and points align with midpoint of vertebral centra.

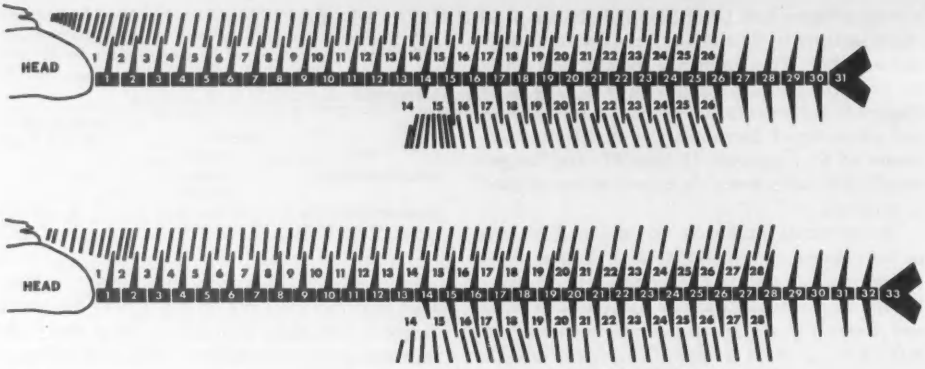


FIGURE 3.—Schematic representation of the relationship of dorsal and anal fin pterygiophores to the vertebral column in adult *Coryphaena hippurus* (upper) and *C. equiselis* (lower). Black numbers, interneural and interhaemal spaces; white numbers, centra.

FIGURE 4.—Number of pterygiophores in the first interneural space in relation to length in 192 *Coryphaena equiselis* (8.6-173, 314 mm SL) and 193 *C. hippurus* (8.6-176 mm SL). For explanation of symbols, see Figure 1.

with the termination of the dorsal fin pterygiophores, complete separation for the two species resulted (Figure 3, Table 3).

Dorsal fin pterygiophores had the same pattern of appearance in both species of *Coryphaena* as the dorsal fin rays. Cartilaginous pterygiophores

TABLE 3.—Adult and juvenile position of posteriormost dorsal and anal fin pterygiophores in their interneural and interhaemal spaces for 193 *Coryphaena hippurus* (9.0-176 mm SL) and 186 *C. equiselis* (8.9-172, 314 mm SL). For numbering of vertebrae and spaces, see Figure 3.

	Interneural space numbers / Interhaemal space numbers										
Species	26/25	26/26	26/27	27/26	27/27	27/28	28/27	28/28	28/29	29/28	29/29
C. hippurus	2	172	3	11	5						
C. equiselis						2	2	172	1	4	5

without rays were first seen in the 22d-24th myomeres at 5.9 mm NL in *C. hippurus* (Figure 2) and with some rays in the 18th-27th myomeres at 6.5 mm NL in the smallest available but more advanced *C. equiselis*. In both species of *Coryphaena* the pterygiophores appeared shortly before the fin rays developed. As pterygiophores were added, anteriorly and posteriorly rays were lacking for one or two anteriormost and posteriormost additions (Figure 2).

In both species, the posteriormost interneural spaces (numbers 26-28) were occupied with pterygiophores between 7 and 8.5 mm SL (Table 4). The anteriormost interneural space started to fill with pterygiophores at 9.3 mm SL in *C. equiselis* and at 13.1 mm SL in *C. hippurus* (Figure 4, Table 4). Adult counts in the anteriormost interneural space of 7-11 pterygiophores were obtained for *C. equiselis* between 12.3 and 23.2 mm SL and for *C. hippurus* of 10-14 pterygiophores between 18.7 and 30.8 mm SL (Figure 4, Table 4).

Ossification of the pterygiophores started in the same area and proceeded in the same directions as the cartilaginous development (Figure 2). Ossification of pterygiophores occurred first at 8.8 mm SL in *C. equiselis* and at 9.7 mm SL in *C. hippurus* (Table 4). The posteriormost interneural space number 28 of *C. equiselis* had ossifying pterygiophores at 8.9 mm SL, and posteriormost interneural space number 26 of *C. hippurus* had ossifying pterygiophores at 10.2 mm SL (Table 4). Specimens 10.3-11.6 mm SL of *C. equiselis*, and 16.2-19.2 mm SL specimens of *C. hippurus* had one or more ossifying pterygiophores in the first interneural space (Figure 4, Table 5). All dorsal fin pterygiophores were ossifying in both species at about 45 mm SL when the count of ossifying pterygiophores was in the adult range and the first interneural space did not have anterior cartilaginous pterygiophores (Figures 4, 5).

TABLE 4.—Development of dorsal fin pterygiophores in the interneural spaces for 105 *Coryphaena hippurus* and 53 *C. equiselis*. For numbering interneural spaces, see Figure 3.

Length mm NL or SL	Interneural space numbers with pterygiophores: Anteriormost space no. (x) *C. hippurus*	Anteriormost space no. (x) *C. equiselis*	Posteriormost space no. (x) *C. hippurus*	Posteriormost space no. (x) *C. equiselis*	Interneural space numbers with ossifying pterygiophores: Anteriormost space no. (x) *C. hippurus*	Anteriormost space no. (x) *C. equiselis*	Posteriormost space no. (x) *C. hippurus*	Posteriormost space no. (x) *C. equiselis*	Number of specimens *C. hippurus*	Number of specimens *C. equiselis*
4.5- 5.5	[1]	—	[1]	—	[2]	—	[2]	—	1	—
5.6- 6.5	19-22(20.3)	18	22-25(23.3)	27	[2]	[2]	[2]	[2]	3	1
6.6- 7.5	[1]6-22(17.7)	15	[1]23-27(25.2)	28	[2]	[2]	[2]	[2]	9	1
7.6- 8.5	8-16(12.6)	5-10(7.0)	25-28(25.6)	28	[2]	[2]	[2]	[2]	3	4
8.6- 9.5	5-13(11.5)	1- 3(1.6)	28	28	[2]	[2]4-23(12.0)	[2]	[2]25-28(27.2)	10	7
9.6-10.5	2- 6(3.7)	1	28	28	[2]13-21(16.6)	1- 6(3.4)	[2]25-28(25.6)	28	7	7
10.6-11.5	2- 7(3.2)	1	28	28	[2]11-18(15.1)	1- 2(1.7)	[2]25-28(25.9)	28	9	9
11.6-12.5	2	1	26	28-29(28.2)	9-16(12.0)	1	26	28-29(28.2)	4	5
12.6-13.5	1- 2(1.6)	1	26-27(26.1)	28	4-11(7.7)	1	26-27(26.1)	28	8	1
13.6-14.5	1- 2(1.1)	1	26-27(26.1)	28	3- 9(4.3)	1	26-27(26.1)	28	9	1
14.6-15.5	1	1	26-27(26.4)	28	2- 4(2.8)	1	26-27(26.4)	28	10	1
15.6-16.5	1	1	26-27(26.1)	28	1- 3(2.0)	1	26-27(26.1)	28	7	5
16.6-17.5	1	1	26	28-29(28.3)	1- 2(1.3)	1	26	28-29(28.3)	7	3
17.6-18.5	1	1	26-27(26.1)	28	1	1	26-27(26.1)	28	7	5
18.6-19.5	1	1	26-27(26.1)	28	1- 2(1.1)	1	26-27(26.1)	28	7	3
19.6-20.5	1	—	26	—	1	—	26	—	4	—

[1]No pterygiophores developed.
[2]No pterygiophores ossified.

TABLE 5.—Sum (adult count) of anal fin pterygiophores in the two anteriormost interhaemal spaces, numbers 14 and 15, in 35 *Coryphaena hippurus* (49.9-176 mm SL) and 32 *C. equiselis* (74.1-172, 314 mm SL). For numbering interhaemal spaces, see Figure 3.

Species	Number of pterygiophores						
	4	5	6	7	8	9	10
C. hippurus				14	18	2	1
C. equisells	5	20	6	1			

Morphology and Development

The pterygiophores in the center area of the dorsal fin developed first in both species. A pterygiophore (proximal and distal radial) appeared as one elongate piece of cartilage (Figure 6). Ossification was first observed at the middle part of the pterygiophore cartilage (Figure 6) and proceeded distally and proximally along the cartilage until only cartilage tips were present at the extremities. At this point, the sagittal and lateral keels began to develop (Figure 4). Further development of the pterygiophore consisted of growth of the keels, growth of bone around the locus of secondary fin ray association, and segregation and ossification of the distal radial. The distal radial developed from the distal tip of the pterygiophore cartilage late during ontogeny (Figure 6), and ossified into two pieces of bone (Figure 7).

The pterygiophores in the posteriormost area of the dorsal fin developed similarly to those of the center area. The posteriormost pterygiophore supported one ray in series. This ray developed from two rays but was counted as one according to Hubbs and Lagler (1958). In adults, the base of the anterior ray fitted closely over the base of the posterior ray and the base of the posterior ray articulated with the distal radial of the posteriormost pterygiophore (Figures 8, 9).

The supports of the anterior portion of the dorsal fin developed last. In *C. equiselis* the first interneural space was almost filled with cartilaginous pterygiophores, but in equal-sized *C. hippurus* the first interneural space was empty and the second interneural space had only one cartilaginous pterygiophore (Figures 10, 11). The anteriormost cartilaginous pterygiophores always had

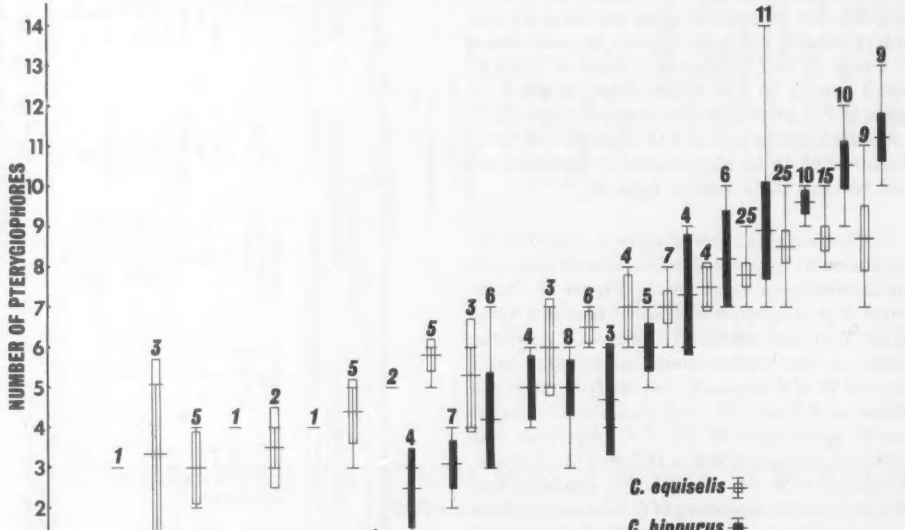


FIGURE 5.—Number of ossifying pterygiophores in the first interneural space in relation to length in 126 *Coryphaena equiselis* and 88 *C. hippurus*. For explanation of symbols see Figure 1.

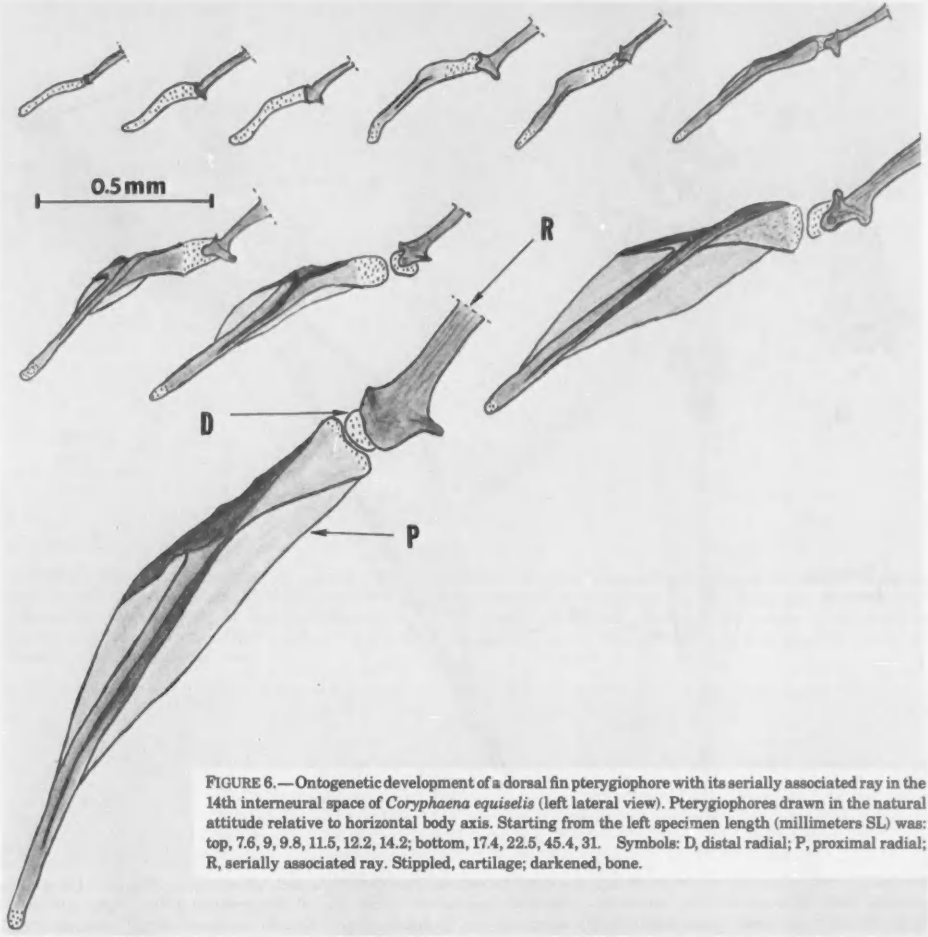


FIGURE 6.—Ontogenetic development of a dorsal fin pterygiophore with its serially associated ray in the 14th interneural space of *Coryphaena equiselis* (left lateral view). Pterygiophores drawn in the natural attitude relative to horizontal body axis. Starting from the left specimen length (millimeters SL) was: top, 7.6, 9, 9.8, 11.5, 12.2, 14.2; bottom, 17.4, 22.5, 45.4, 31. Symbols: D, distal radial; P, proximal radial; R, serially associated ray. Stippled, cartilage; darkened, bone.

a ray developing concurrently (Figures 2, 10, 11). In specimens of both species, which had the full count of pterygiophores in the first interneural space, it was common to have a ray develop in front of the cartilaginous pterygiophore (Figure 2). The pterygiophores of the first interneural space in large juveniles and adults of both species were vertical to the body axis near the first neural spine and slightly anteriorly inclined dorsad near the head (Figure 12). The anteriormost pterygiophore in the adults was either of normal size (not figured), very small (Figures 12, 13), or just a vestige (not figured). In a few instances, in both species, the anteriormost pterygiophore was completely or partially fused to the second pterygiophore. The anteriormost pterygiophore of both species had either one, two, or three associated rays (Table 2). For the two species the anteriormost dorsal fin ray was either normal in size or a vestige (Figures 12, 13). In both species three types of first fin ray vestiges were observed: a paired vestige (Figure 13), a single right vestige, and a single left vestige.

Distal radials were present between the bases of each fin ray for almost the entire dorsal fin. Distal radials were last to ossify from the distal portion of the pterygiophore cartilage. Only the anteriormost three fin rays of both species sometimes

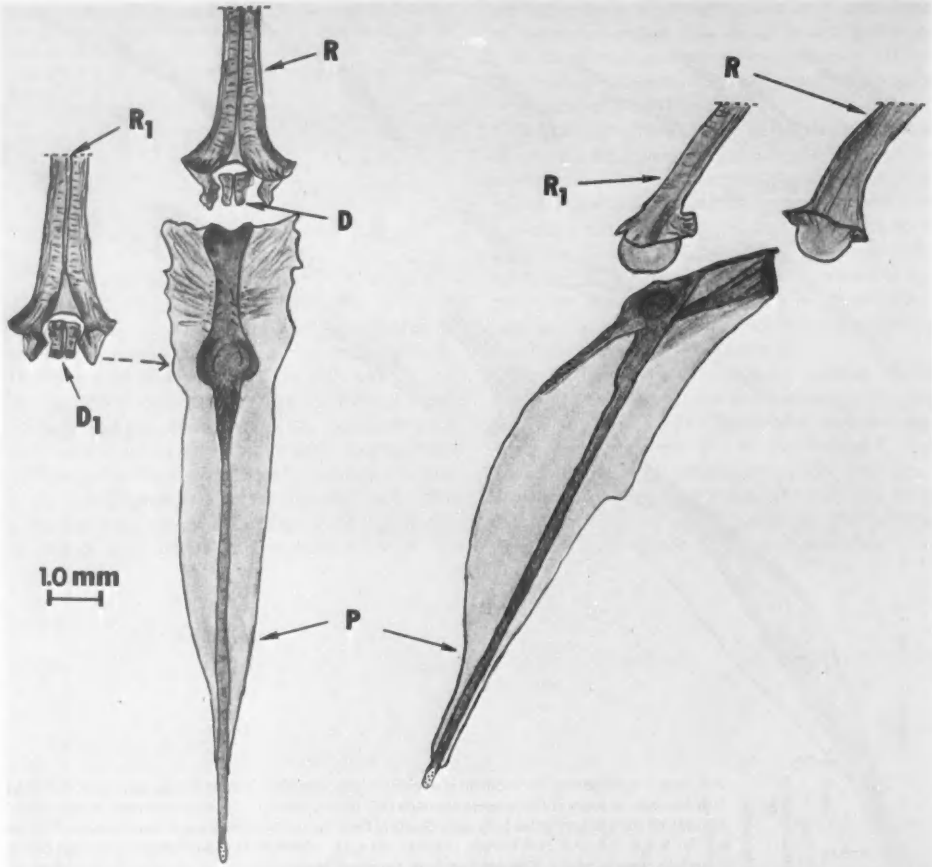


FIGURE 7.—Pterygiophore from 14th interneural space with its secondarily and serially associated rays from a 230 mm SL *Coryphaena equiselis*. Left: anterodorsal view, secondarily associated ray moved to the right of the proximal radial; right: left lateral view. Symbols: D_1, distal radial of secondarily associated ray; D, distal radial of serially associated ray; P, proximal radial; R_1, secondarily associated ray; R, serially associated ray. Stippled, cartilage; darkened, bone.

lacked distal radials. The absence or presence of distal radials was not related to the number of fin rays associated with the anteriormost pterygiophore (Table 2). The first three or four (anteriormost) distal radials of both species differed in structure from the remainder. These radials consisted of one piece of bone (Figure 14) whereas all other radials were of two pieces (Figures 7, 8).

The dorsal pterygiophores of *Coryphaena* spp. differed in several ways from other perciform fishes. Predorsal bones reported in Apogonidae (Fraser 1972), Serranidae and Grammistidae (Kendall 1976), Sparidae (Houde and Potthoff 1976), and for all the stromateoid families (Ahlstrom et al. 1976) were lacking. Also lacking was the terminal bone in the dorsal fin support series called a "stay" by Weitzman (1962). Stays have been reported for such families as Characidae (Weitzman 1962), Scombridae (Kramer 1960; Potthoff 1975), Sparidae (Houde and Potthoff 1976), Nomeidae and Centrolophidae (Ahlstrom et al. 1976), and Centropomidae, Kyphosidae, Lutjanidae, Percichthyidae, and Scorpidae (Johnson 1978). A stay was observed in the Scombrolabracidae and a double stay in the Gempylidae (Potthoff et al. 1980).

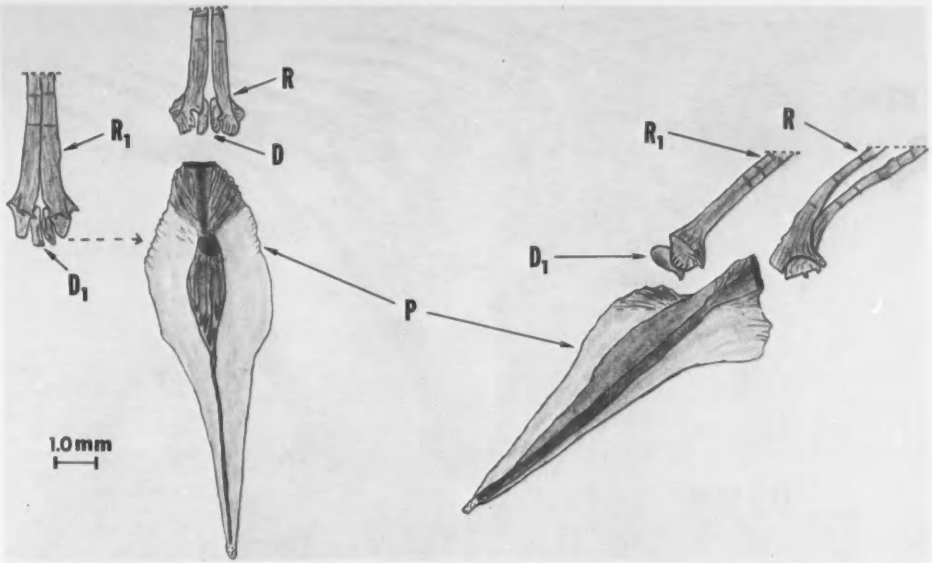


FIGURE 8.—Posteriormost dorsal fin pterygiophore with its secondarily and serially associated rays from a 230 mm SL *Coryphaena equiselis*. Left: anterodorsal view, secondarily associated ray has been moved to the right of the proximal radial; right: left lateral view, pterygiophore has been tilted 30° from the horizontal toward the vertical. Symbols: D_1, distal radial of secondarily associated ray; D, distal radial of serially associated double ray; P, proximal radial; R_1, secondarily associated ray; R, serially associated double ray. Stippled, cartilage; darkened, bone.

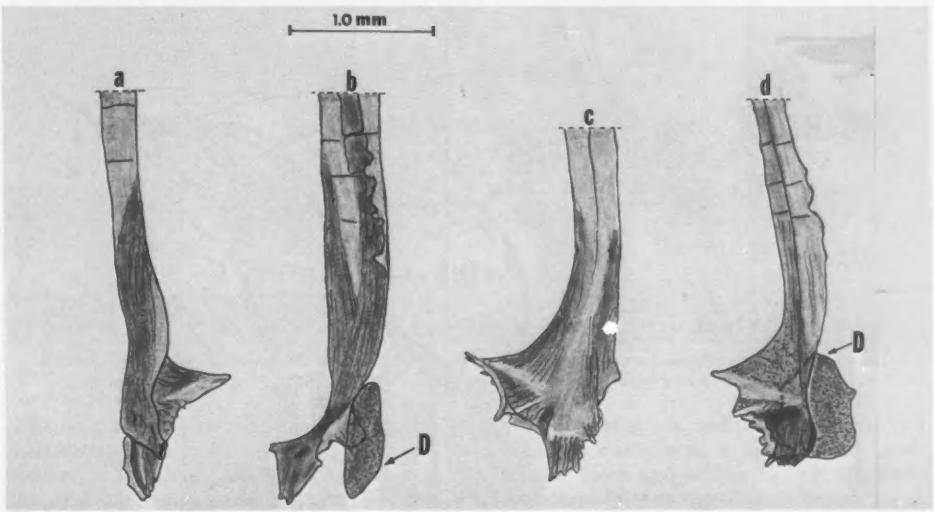


FIGURE 9.—Anterior and right lateral views of right side of a disarticulated posteriormost double dorsal fin ray with its distal radial from a 230 mm SL *Coryphaena equiselis*. a, right half of anterior ray, anterior view; b, right half of posterior ray and right half of its distal radial, anterior view; c, right half of anterior ray, lateral view; d, right half of posterior ray and right half of its distal radial, lateral view. Symbol: D, distal radial.

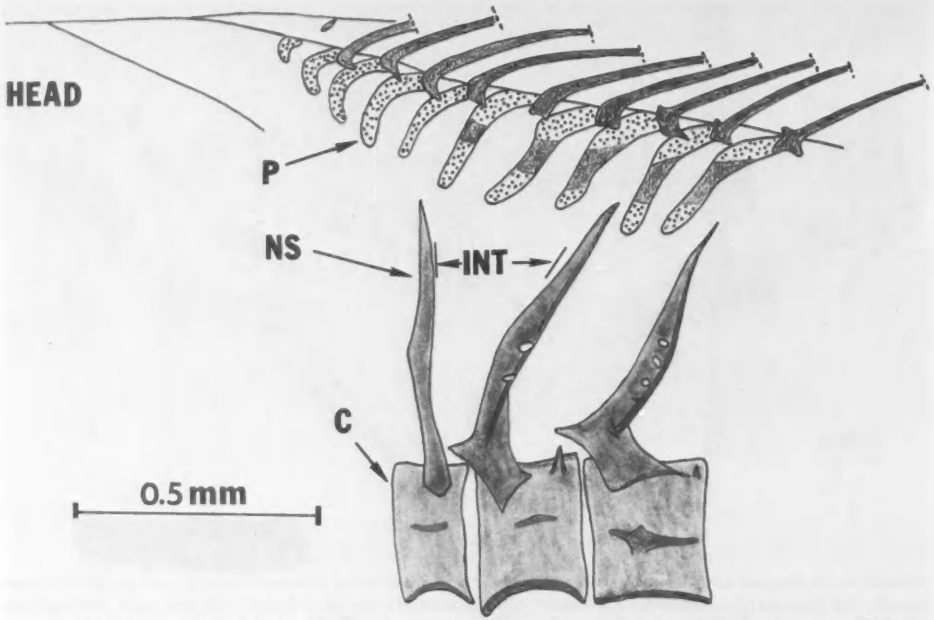


FIGURE 10.—Left lateral view of anteriormost part of the dorsal fin and pterygiophores for a 11 mm SL *Coryphaena equiselis*, showing relationship of pterygiophores to head, interneural spaces, and centra. Symbols: C, first centrum; INT, second interneural space; NS, first neural spine; P, proximal radial. Stippled, cartilage; darkened, bone.

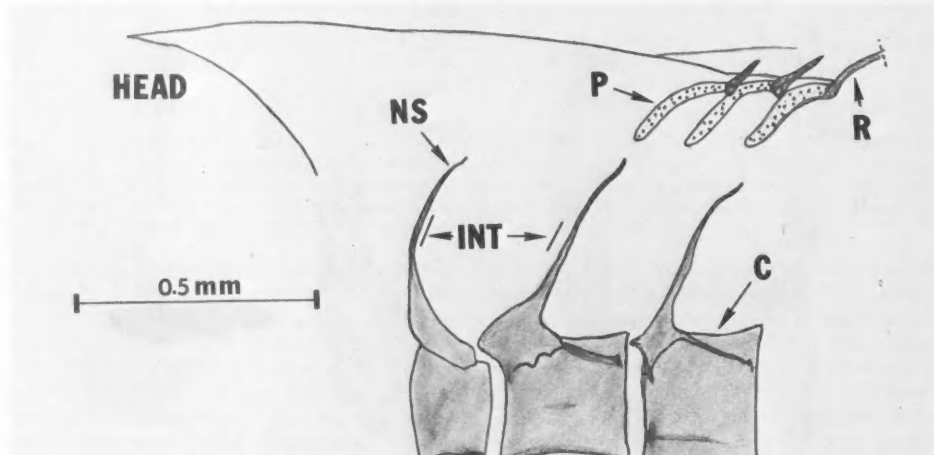


FIGURE 11.—Left lateral view of anteriormost part of the dorsal fin and pterygiophores for a 11 mm SL *Coryphaena hippurus*, showing the relationship of pterygiophores to head, interneural spaces, and centra. Symbols: C, third centrum; R, dorsal fin ray. For explanation of other symbols, see Figure 10. Stippled, cartilage; darkened, bone.

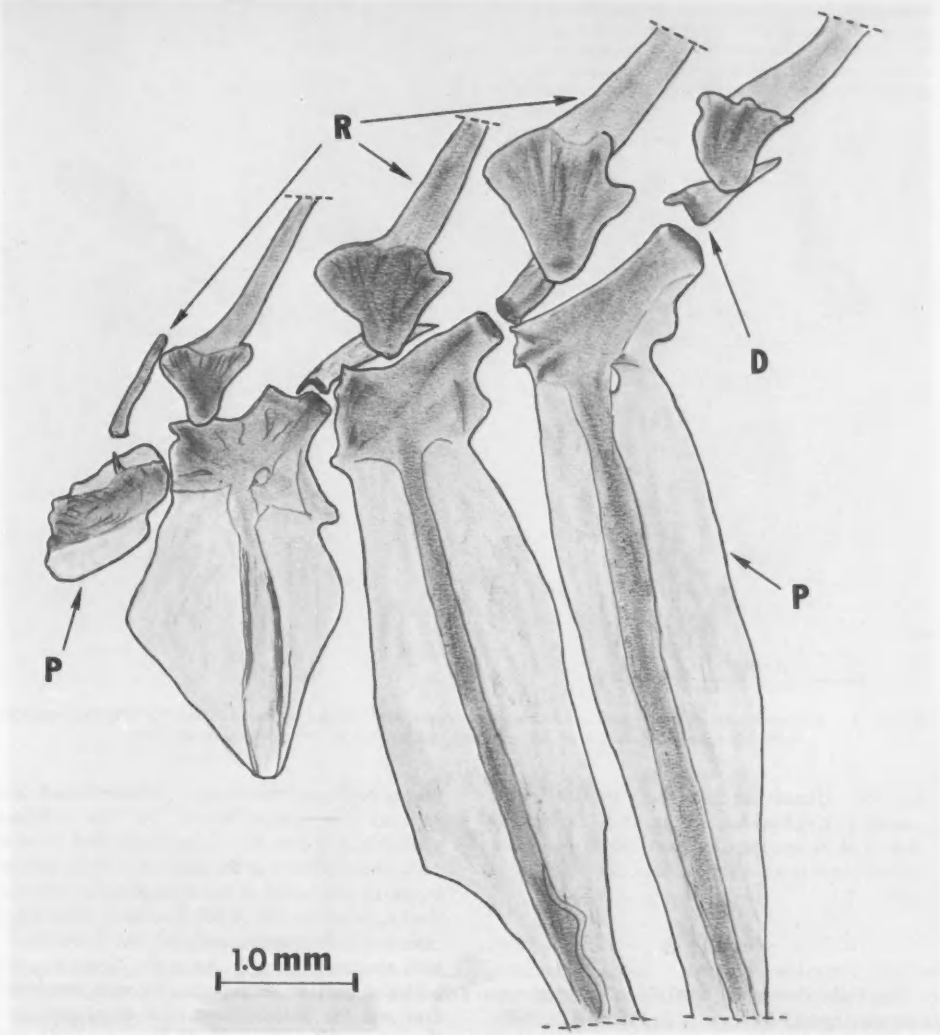


FIGURE 12.—Left lateral view of four anteriormost dorsal fin pterygiophores with secondarily and serially associated rays from a 230 mm SL *Coryphaena equiselis*. Symbols: R, dorsal fin ray; P, proximal radial; D, distal radial.

The proximal and distal radials (except the anteriormost three or four) of *Coryphaena* spp. were similar along the entire fin and were located between the bifurcate bases of the fin rays. Middle radials were absent in the posterior portion of the fin. In most other perciform fishes, distal radials differ between the first and second dorsal fins. The first dorsal fin distal radials are anterior to the bases of the fin spines, and the second dorsal fin distal radials are between the bifurcate bases of the fin rays, and middle radials are present posteriorly. Anatomically different distal radials for the first and second dorsal fins and the presence of middle radials posteriorly have been reported in the Carangidae (Berry 1969), Scombridae (Kramer 1960; Potthoff 1974, 1975),

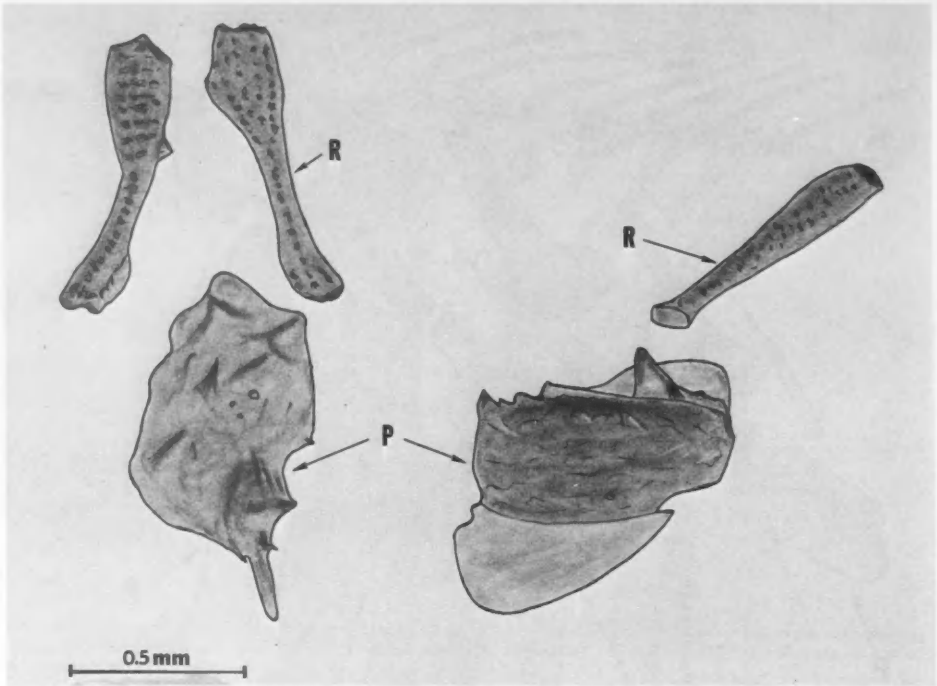


FIGURE 13.—Anteriormost dorsal fin pterygiophore with secondarily associated vestigial ray from a 230 mm SL *Coryphaena equiselis*. Left: anterodorsal view, right: left lateral view. Symbols: P, proximal radial; R, vestigial ray.

Sparidae (Houde and Potthoff 1976), Centropomidae, Kyphosidae, Lutjanidae, Percichthyidae, and Scorpidae (Johnson 1978), and Gempylidae and Scombrolabracidae (Potthoff et al. 1980).

Anal Fin

The fully developed anal fin of *Coryphaena hippurus* has 25-31 rays (N = 147, $\bar{x}$ = 28, SE = 0.01, 16-172 mm SL) and that of *C. equiselis* 23-29 (N = 118, $\bar{x}$ = 26, SE = 0.01, 16-230 mm SL). The anal fin ray counts, in contrast to the dorsal fin ray counts, differ only slightly from those reported by Gibbs and Collette (1959), Rothschild (1964), and Shcherbachev (1973). Both species have adult anal fin ray counts at smaller sizes than dorsal fin ray counts (*C. hippurus* at 8-11 mm SL, *C. equiselis* at 8-9 mm SL).

Anal fin rays were first seen in some *C. hippurus* at 6 mm NL, just before the onset of dorsal fin ray development and all *C. hippurus* had anal rays at 7 mm NL (Figure 15). The smallest available (6.5 mm NL) *C. equiselis* had 14 anal rays. Development of the anal fin of both species began in the finfold at the approximate center of the fin, below the 22d or 23d myomere. Addition of rays was in an anterior and posterior direction for both species (Figure 2). As in the dorsal fin, the posterior portion of the anal fin was completed first and the anteriormost rays developed last. From 6 mm NL to 9 mm SL, *C. hippurus* had fewer anal fin rays than *C. equiselis*; at 10 and 11 mm SL, both species had about equal numbers of rays; at 12 mm SL and longer, *C. hippurus* tended to have more anal rays than *C. equiselis* (Figure 15).

Appearance and additional sequence of anal fin rays in *Coryphaena* spp. are similar to *Scomber japonicus* (*Pneumatophorus diego*) (Kramer 1960), *Thunnus atlanticus* (Potthoff 1975), *Haemulon plumieri* (Saksena and Richards 1975), and *Archosargus rhomboidalis* (Houde and Potthoff 1976).

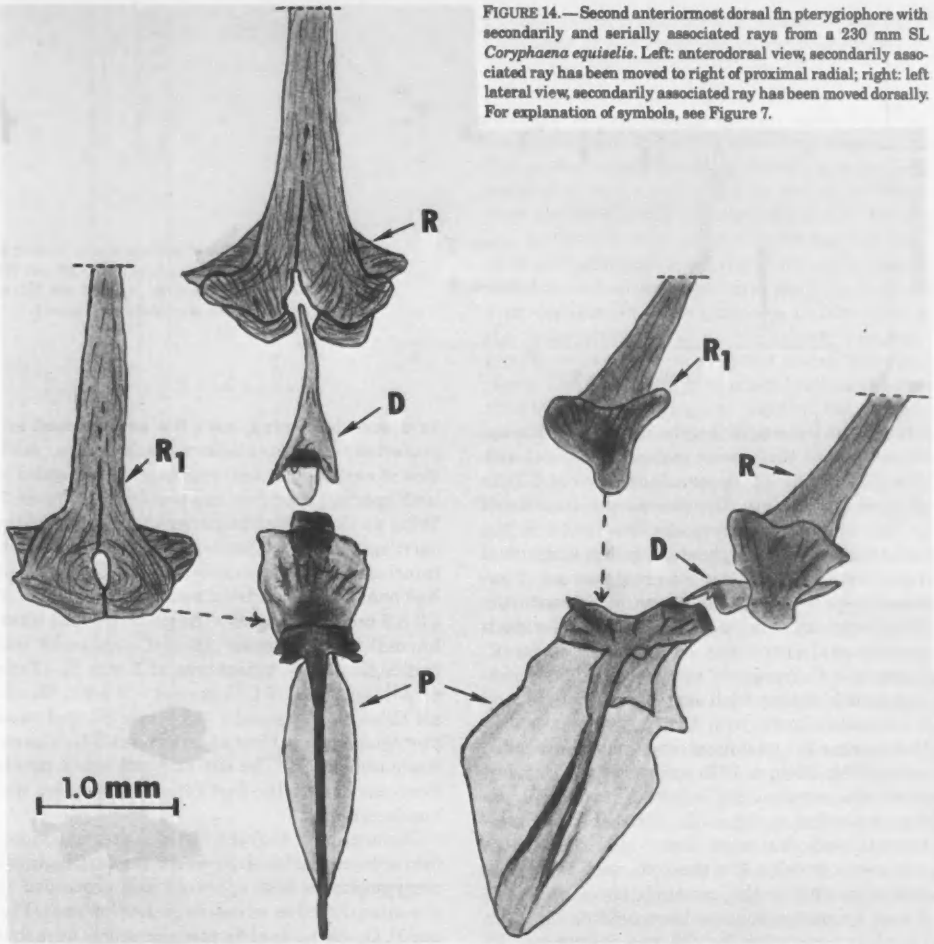


FIGURE 14.—Second anteriormost dorsal fin pterygiophore with secondarily and serially associated rays from a 230 mm SL *Coryphaena equiselis*. Left: anterodorsal view, secondarily associated ray has been moved to right of proximal radial; right: left lateral view, secondarily associated ray has been moved dorsally. For explanation of symbols, see Figure 7.

For *Trachurus symmetricus*, Ahlstrom and Ball (1954) reported an anterior to posterior anal fin development.

Anal Fin Pterygiophores

Counts

The description for dorsal fin pterygiophores in the foregoing section may be applied to anal fin pterygiophores because of the similarities between the two fins and their supports. Pterygiophores of the anal fin are inserted in the interhaemal spaces. The anteriormost (first) interhaemal space is bounded anteriorly by the stomach, intestine, and anus and posteriorly by the first haemal spine. The first haemal spine was of variable length, and in many cases did not reach the anal fin pterygiophores. The anal fin pterygiophores in the two anteriormost interhaemal spaces were therefore summed (Table 5, Figure 3).

Fully developed specimens of *Coryphaena* spp. differed in their numbers and arrangement of anal fin pterygiophores. The total number of pterygiophores closely approximated the anal fin ray count. For both species the pterygiophore count was equal to or one to two less than the anal fin ray count. The sum of the pterygiophores found in the

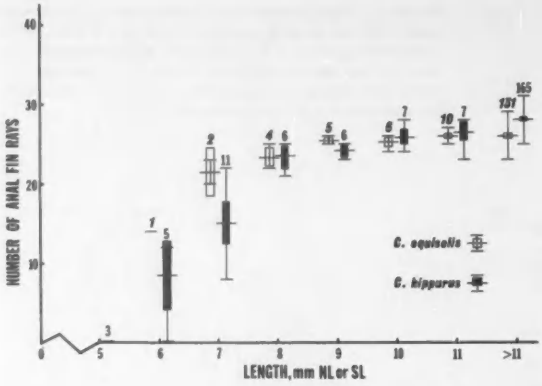


FIGURE 15.—Number of anal fin rays in relation to length in 159 *Coryphaena equiselis* (6.5-230 mm NL or SL) and 210 *C. hippurus* (5.0-230 mm NL or SL). For explanation of symbols, see Figure 1.

first two anteriormost interhaemal spaces (14 and 15) separated the species most of the time, with 7-10 ($\bar{x}$ = 8.0) for *C. hippurus* and 4-7 ($\bar{x}$ = 5.0) for *C. equiselis* (Table 5). The two species also differed in the number of pterygiophores found in the remainder of the interhaemal spaces. Individual variability, however, was too great for each interhaemal space to serve as a separating character. The mean number of pterygiophores for each interhaemal space was always greater for *C. hippurus*. *Coryphaena equiselis* had more interhaemal spaces with one pterygiophore and *C. hippurus* more with two pterygiophores. In *C. hippurus* the anal fin pterygiophores extended to the 25th, 26th, or 27th interhaemal space, but most often to the 26th, whereas in *C. equiselis* they extended to the 27th, 28th, or 29th interhaemal space, but most often to the 28th. There was some overlap for the two species in this character, but if the termination of anal and dorsal fin pterygiophores is considered together, complete separation for the two species results (Table 3). The dorsal and anal fin pterygiophores most often terminated in opposing interneural and interhaemal spaces (Table 3).

Morphology and Development

Cartilaginous anal fin pterygiophores without fin rays were first observed in the 18th-24th myomeres (which approximately correspond to the 18th-24th interhaemal spaces) in a 5.9 mm NL *C. hippurus* (Figure 2, Table 6), but rays were developing in a 6 mm NL specimen. The smallest available *C. equiselis* of 6.5 mm NL had cartilaginous pterygiophores in myomeres 18-27. Fin rays were developing, but a few anteriormost and posteriormost pterygiophores lacked rays. Addition of cartilaginous pterygiophores proceeded in both species anteriorly and posteriorly (Figure 2, Table 6). Rays developed after the addition of the cartilaginous pterygiophores. The posteriormost interhaemal space number 26 of *C. hippurus* had one to three cartilaginous pterygiophores at 7.3-8.3 mm SL (Table 6). The posteriormost interhaemal space number 28 of *C. equiselis* had cartilaginous pterygiophores at 7 mm SL (Table 6). All specimens of *C. hippurus* > 9.5 mm SL and all those of *C. equiselis* > 8.5 mm SL had some pterygiophores in their anteriormost interhaemal space number 14. The size at which adult counts were reached for the first interhaemal space was not determined.

Ossification of the cartilaginous pterygiophores first occurred in the area where the cartilaginous pterygiophores first appeared and proceeded in the same direction as cartilage development (Figure 2). Ossifying anal fin pterygiophores were first seen at 8.8 mm SL in *C. equiselis* and at 9.7 mm SL in *C. hippurus* in the 16th-19th and 16th-25th interhaemal spaces (Table 6), and concurrently with ossifying dorsal fin pterygiophores. The posteriormost interhaemal space number 28 of *C. equiselis* had ossifying pterygiophores at 8.9 mm SL and space number 26 of *C. hippurus* had them at 10.2 mm SL (Table 6). All specimens of *C. equiselis* > 9.4 mm SL and all specimens of *C. hippurus* > 11 mm SL had some ossifying pterygiophores in the anteriormost interhaemal space number 14, or rarely space number 15 (Table 6). The anteriormost anal fin pterygiophore was ossifying in *C. equiselis* at 14.9-22 mm SL and in

TABLE 6.—Development of anal fin pterygiophores in the interhaemal spaces for 46 *Coryphaena hippurus* and 34 *C. equiselis*. For numbering interhaemal spaces, see Figure 3.

Length mm NL or SL	Interhaemal spaces with cartilaginous pterygiophores				Interhaemal spaces with ossifying pterygiophores				Number of specimens	
	Anteriormost space no. (*x*)		Posteriormost space no. (*x*)		Anteriormost space no. (*x*)		Posteriormost space no. (*x*)			
	C. hippurus	*C. equiselis*	*C. hippurus*	*C. equiselis*	*C. hippurus*	*C. equiselis*	*C. hippurus*	*C. equiselis*	*C. hippurus*	*C. equiselis*
4.6- 5.5	[1]	—	[1]	—	[1]	—	[1]	—	1	—
5.6- 6.5	18-22(19.7)	18	23-24(23.7)	27	[1]	[1]	[1]	[1]	3	1
6.6- 7.5	14-20(17.3)	15	23-26(25.1)	28	[1]	[1]	[1]	[1]	9	1
7.6- 8.5	14-16(14.6)	15-16(15.5)	25-26(25.7)	28	[1]	[1]	[1]	[1]	3	4
8.6- 9.5	14-15(14.4)	14	26	28	[1]	[2]14-16(14.8)	[1]	[2]19-28(26.0)	10	7
9.6-10.5	14	14-15(14.1)	26	28	[2]14-16(15.4)	14-15(14.1)	[2]25-26(25.8)	28	7	7
10.6-11.5	14	14-15(14.1)	26	28	[2]14-18(14.7)	14-15(14.1)	[2]25-26(25.9)	28	9	9
11.6-12.5	14	14	26	28-29(28.2)	14	14	26	28-29	4	5

[1]No pterygiophores developed.
[2]No pterygiophores ossified.

C. hippurus at 17.2-30 mm SL. The development of individual anal fin pterygiophores was similar to that of the dorsal fin pterygiophores.

Each anal fin pterygiophore of both species had two rays; one ray was in a serial association and the preceding ray was in a secondary association. The posteriormost anal ray lacked a secondary association with a pterygiophore and the anteriormost anal ray lacked a serial association (Figure 16). Exceptions were common with the anteriormost pterygiophore and rays. Many specimens of both species had very small first pterygiophores or even vestiges. In a few instances in both species the anteriormost first pterygiophore was completely or partially fused to the second pterygiophore. The normal number of anal rays associated with the first pterygiophore was two, but for both species one or three rays also were found. The anteriormost anal ray was either normal as in Figure 16, very small, or a vestige. As in the dorsal fin, the vestige was either single left or right, or paired.

A distal radial was present between the base of each fin ray almost for the entire anal fin. It developed and ossified from the pterygiophore cartilage. Only the anteriormost anal fin ray sometimes did not have a distal radial between its base (Table 7). Only 1 *C. hippurus* out of 49 had two anteriormost rays without distal radials. When the anteriormost ray had a distal radial, it was either serially or secondarily associated with the first pterygiophore. When the association was serial, the anteriormost pterygiophore had only one ray; when it was secondary, it had two rays. It is possible that, when the association was secondary, the distal radial of the first fin ray was in actuality a vestigial pterygiophore. The specimen in Figure 16 did not have a distal radial for the anteriormost ray. The absence or presence of distal radials for the anteriormost anal fin ray was not related to the number of fin rays that were

TABLE 7.—Number (adult count) of anteriormost anal fin rays without distal radials and number of anal fin rays associated secondarily and serially with the anteriormost anal fin pterygiophore in 49 *Coryphaena hippurus* (41.0-176 mm SL) and 33 *C. equiselis* (74.1-172, 314 mm SL).

Item	Species	Number of anteriormost anal fin rays			
		0	1	2	3
Without distal radials	*C. hippurus*	24	24	1	
	C. equiselis	10	23		
Associated with the anteriormost anal pterygiophore	*C. hippurus*		3	40	6
	C. equiselis		3	29	1

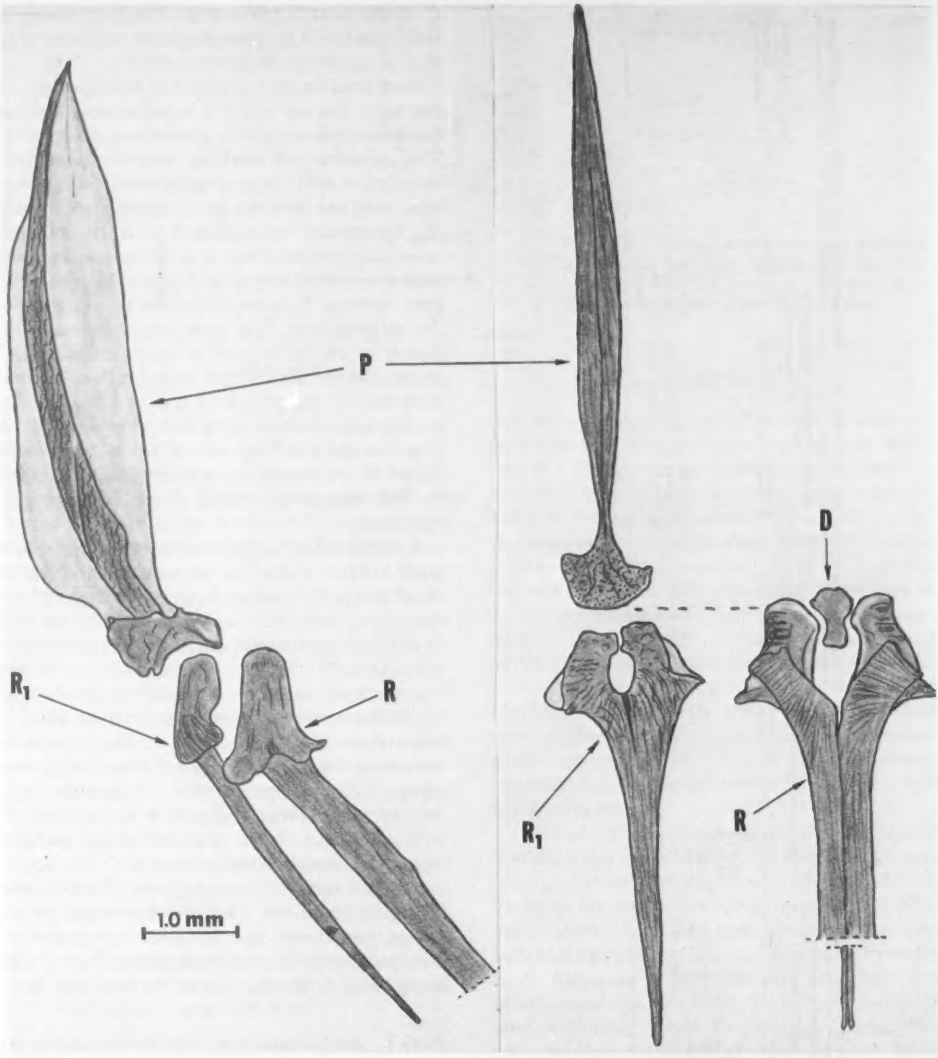


FIGURE 16.—Anteriormost anal fin pterygiophore with secondarily and serially associated rays from a 230 mm SL *Coryphaena equiselis*. Left: left lateral view; right: anterior view, serially associated ray has been moved to the left of the proximal radial. • Symbols: D, distal radial of serially associated ray; P, proximal radial; R_1, secondarily associated ray; R, serially associated ray.

associated with the anteriormost anal pterygiophore (Table 7). In both species either one, two, or three rays were associated with the first pterygiophore. In both species the anteriormost distal radial (which was either between the base of the first or second anal fin ray) was a single piece of bone (Figure 16). The second distal radial (which was either between the base of the second or third anal fin ray) consisted of two pieces of bone, as shown for the dorsal pterygiophores in Figures 7

and 8. The two pieces of the second distal radial were sometimes partially fused; and in a few rare cases, the second distal radial was one piece of bone. All following distal radials of the anal fin were two pieces of bone in both species. The posteriormost anal fin ray consisted of two closely approximated rays with one distal radial.

TABLE 8.—Adult caudal fin ray counts for 117 *Coryphaena hippurus* (19.6-172 mm SL) and 97 *C. equiselis* (19.6-230 mm SL). Symbols: USCR, upper secondary caudal rays; LSCR, lower secondary caudal rays; PCR, principal caudal rays.

Total fin ray count	USCR+PCR+LSCR	Number of specimens	
		C. hippurus	*C. equiselis*
37	10+17+10	0	1
38	10+17+11	2	1
39	10+17+12	0	2
39	11+17+11	10	0
40	11+17+12	12	28
40	12+17+11	3	0
41	11+17+13	0	6
41	12+17+12	36	17
42	12+17+13	23	32
43	13+17+13	26	8
44	13+17+14	2	2
45	14+17+14	3	0

Caudal Fin

The two species differed little in ray counts on fully developed caudal fins. *Coryphaena hippurus* had 38-45 ($\bar{x}$ = 41.4) caudal rays and *C. equiselis* had 37-44 ($\bar{x}$ = 41.1) (Table 8). *Coryphaena hippurus* tended to have an equal number of upper and lower secondary caudal rays whereas *C. equiselis* tended to have one or two more lower than upper secondary caudal rays. Adult caudal ray counts for *C. hippurus* were obtained between 15.6 and 19.6 mm SL and for *C. equiselis* between 11.6 and 12.5 mm SL (Tables 9, 10). A procur-

TABLE 9.—Caudal fin ray development in 201 *Coryphaena hippurus* (5.0 mm NL-172 mm SL) and 138 *C. equiselis* (6.5 mm NL-230 mm SL). Symbols: SCR, secondary caudal rays; PCR, principal caudal rays.

Length mm NL or SL	*Coryphaena hippurus*								*Coryphaena equiselis*							
	Upper		Lower		Total fin ray count				Upper		Lower		Total fin ray count			
	SCR	PCR	PCR	SCR	Range	$\bar{x}$	$S_{\bar{x}}$	*N*	SCR	PCR	PCR	SCR	Range	$\bar{x}$	$S_{\bar{x}}$	*N*
4.6- 5.5	0	2-4	2-5	0	4- 9	7.0	1.5	3	—	—	—	—	—	—	—	—
5.6- 6.5	0	4-8	5-8	0	9-16	11.3	1.6	4	0	6	6	0	12	—	—	1
6.6- 7.5	0	1-8	2-8	0- 1	3-17	12.9	1.3	10	0	9	8	1- 2	18-19	18.5	0.5	2
7.6- 8.5	0	9	8	1- 2	18-19	18.8	0.2	6	0- 3	9	8	2- 4	19-24	21.2	1.2	5
8.6- 9.5	0- 3	9	8	2- 4	19-24	19.8	1.1	5	3- 8	9	8	4- 8	24-33	29.0	1.9	4
9.6-10.5	1- 4	9	8	2- 5	21-26	23.3	0.7	7	5- 9	9	8	6- 9	28-35	31.0	1.3	5
10.6-11.5	0- 4	9	8	2- 5	19-26	24.7	1.0	7	7- 9	9	8	8- 9	32-35	33.6	0.4	7
11.6-12.5	4- 5	9	8	5- 7	26-29	27.7	0.9	3	10-11	9	8	11-12	38-40	38.5	0.5	4
12.6-13.5	5- 6	9	8	6	26-29	28.6	0.2	5	11	9	8	12	40	—	—	1
13.6-14.5	7- 8	9	8	8- 9	32-34	33.3	0.3	6	11	9	8	12	40	—	—	1
14.6-15.5	7- 9	9	8	8-10	32-36	34.7	0.6	6	12	9	8	12	41	—	—	1
15.6-16.5	9-11	9	8	10-12	36-40	37.5	0.7	6	11	9	8	11-13	39-41	40.0	1.0	2
16.6-17.5	9-11	9	8	9-11	35-39	36.6	0.7	5	11	9	8	11-13	39-41	40.0	0.6	3
17.6-18.5	9-11	9	8	9-11	35-39	38.2	0.8	5	11-12	9	8	12-13	40-42	40.5	0.5	4
18.6-19.5	8-12	9	8	12	37-41	39.5	0.6	6	11	9	8	12	40	—	—	1
>19.5	10-14	9	8	11-14	38-45	41.4	0.1	117	10-13	9	8	10-14	37-44	41.1	0.1	97

TABLE 10.—Length (in millimeters NL or SL) at which parts of the caudal complex first appear in cartilage and then ossify in 41 *Coryphaena hippurus* (5.0 mm NL-110 mm SL) and 39 *C. equiselis* (6.5-85 mm SL). "First appearance in cartilage" does not pertain to all specimens of that size but only indicates a first appearance. Symbol: Pu, preural centrum.

Part	*Coryphaena hippurus*				*Coryphaena equiselis*			
	First appearance in cartilage	First evidence of ossification	Ossifying in all specimens	Completely fused	First appearance in cartilage	First evidence of ossification	Ossifying in all specimens	Completely fused
Neural spine, Pu_3	7.4	9.5	11.9	—	>6.5 but <7.6	7.6	8.1	—
Specialized neural arch, Pu_2	7.4	11.9	11.9	—	>6.5 but <7.6	9.5	9.5	—
Large uroneural	—	8.0-10.6	11.9	75.0- 85.0	—	>6.5 but < 7.6	7.6	75.0-80.0
Small uroneural	—	11.9	11.9		—	(9.5?) 10.8	10.8	
Epurals	7.4-8.0	14.6	14.6	40.0- 47.0	>6.5 but <7.6	10.8	10.8	34.0-39.0
Urostyle	—	8.0	11.9	—	—	7.6	7.6	—
Pu_2 centrum	—	9.5	11.9	—	—	7.6	9.5	—
Pu_3 centrum	—	9.5	11.9	—	—	7.6	9.5	—
Haemal spine, Pu_3	6.0	9.5	11.9	—	<6.5	7.6	9.5	—
Haemal spine, Pu_2	5.0	9.5	11.9	—	<6.5	7.6	9.5	—
Parhypural	<5.0	9.5	11.9	—	<6.5	7.6	7.6	—
Hypural 1	<5.0	9.5	11.9	106.0	<6.5	7.6	7.6	69.0
Hypural 2	<5.0	9.5	11.9		<6.5	7.6	7.6	
Hypural 3	<5.0	9.5	11.9	106.0	<6.5	7.6	7.6	69.0
Hypural 4	6.0	9.5	11.9		6.5	7.6	7.6	
Hypural 5	8.1-9.5	11.9	11.9	—	7.6	9.5	9.5	—

rent spur (Johnson 1975) was not observed in either species.

The caudal rays first developed in both species from the midline between hypurals 2 and 3 in preflexion larvae (Figure 17). Rays were added in a posterior and anterior direction (Figure 18). After complete notochord flexure the secondary caudal rays were added in an anterior direction. For equal-sized specimens from 6.5 mm NL to 19.5 mm SL, *C. hippurus* had fewer caudal fin rays than *C. equiselis* (Table 9).

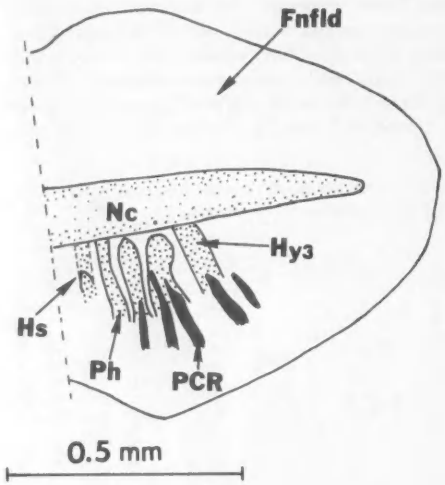


FIGURE 17.—Caudal complex of *Coryphaena hippurus*, 5.0 mm NL. Symbols: Fnfld, finfold; Hs, haemal spine; Hy, hypural; Nc, notochord; PCR, principal caudal ray; Ph, parhypural. Stippled, cartilage; darkened, ossifying bones or rays.

Caudal Fin Supports

The caudal fin rays of *Coryphaena* spp. were supported by some of the bones of the caudal complex. Three posteriormost centra were involved in this support. In 2 out of 97 *C. equiselis* the caudal fin rays were also supported by a fourth centrum. This variation was not observed in *C. hippurus*.

Supporting bones of the caudal complex consisted of three centra (urostyle and preural centra numbers 2 and 3), one neural spine, one specialized neural arch, two autogenous haemal spines, one autogenous parhypural bone, five autogenous hypural bones, two paired uroneural bones, and two epural bones. These parts were seen during development, but not all the parts are readily discerned in the adults due to ontogenetic fusion.

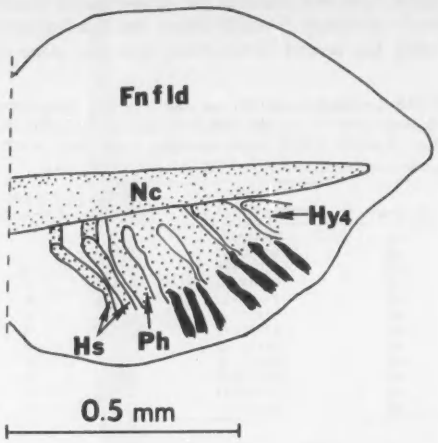


FIGURE 18.—Caudal complex of *Coryphaena hippurus*, 6.0 mm NL. For explanation of symbols, see Figure 17. Stippled, cartilage; darkened, ossifying bones or rays.

The species did not differ in the anatomy of the caudal complex, but they differed in the size at which parts appeared and ossified. The 6.5 mm NL *C. equiselis* was at the same stage of caudal development as a 6.5 mm NL *C. hippurus*. From 7.6 to 16 mm SL, *C. equiselis* was more advanced. Specimens >16 mm SL of both species had the caudal complex equally ossified for the same lengths, but epural, uroneural, and hypural fusions occurred at shorter lengths in *C. equiselis*.

Development of the caudal complex of *C. hippurus* is described here rather than *C. equiselis* because small specimens were not available for *C. equiselis*. Most of the illustrations of the caudal complex are of *C. equiselis* because they were drawn before it was apparent that *C. equiselis* < 7.6 mm were not available. Because both species had identical caudal complex anatomy, no drawings of *C. hippurus*' caudal complex were made for specimens >7.6 mm SL.

At 5 mm NL, *C. hippurus* had a straight notochord. Hypurals 1 to 3, the parhypural, and the haemal spine of the future preural centrum 2 were present in cartilage and 2 + 3 principal caudal rays were counted (Figure 17). At 6 mm NL, hypural 4 and an additional cartilaginous haemal spine of the future preural centrum 3 were present (Figure 18). Notochord flexion in *C. hip-*

purus was between 7 mm NL and 7.5 mm SL, and in *C. equiselis* between 6.5 mm NL and 7.6 mm SL (Figure 19). During the flexion stage of some *C. hippurus* the neural spine of preural centrum 3, the specialized neural arch of preural centrum 2, and the two epurals began to develop from cartilage (Figure 19). Hypural 5 was first seen in cartilage at 8.1 mm SL. The two paired uroneurals did not develop from cartilage—in *C. hippurus* the larger, more ventrally and anteriorly located pair was seen at 8-10.6 mm SL, and the smaller, more dorsally and posteriorly located pair was seen at 11.9 mm SL. Development of the two paired uroneurals occurred at a smaller size in *C. equiselis* (Figure 19 left, Table 10). The smaller uroneural pair gradually fused to the outside of the larger uroneural pair in both species. This fusion was completed between 75 and 85 mm SL for *C. hippurus* and between 75 and 80 mm SL for *C. equiselis* (Table 10). Monod (1968) recognized only one uroneural (stegural) pair in adult *C. hippurus*.

Ossification of the cartilage bones in the caudal complex of *C. hippurus* began with the urostyle at 8 mm SL. Last to ossify at 14.6 mm SL were the two epurals. The ossification sequence of all hypural bones is shown in Table 10. The epurals of *C. hippurus* developed and fused in the same manner as those of *C. equiselis*, although development and fusion were always at a smaller size for *C. equiselis* (Figures 19-23, Table 10). Monod (1968) recognized only one epural for adult *C. hippurus*. In *Coryphaena* spp., hypurals 1 and 2 and hypurals 3 and 4 fused to a dorsal and ventral hypural plate (Figures 20-23, Table 10). During fusion paired bony ventrolateral and dorsolateral articular projections formed on the ventral edge of hypural 3 and on the dorsal edge of hypural 2. These projections became the articulatory surfaces between the dorsal and ventral hypural plates (Figures 20-23). The two hypural plates of *Cory-*

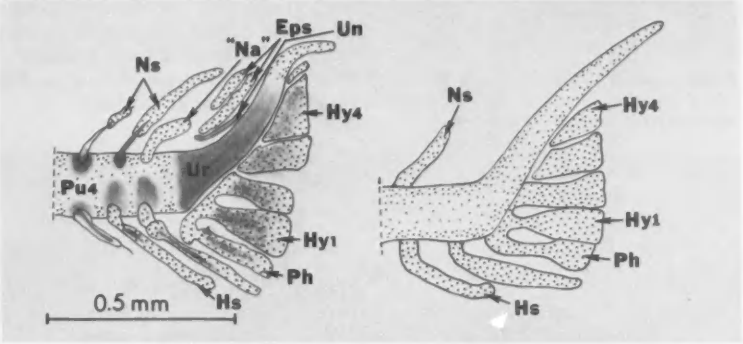


FIGURE 19.—Supporting bones of the caudal complex of *Coryphaena hippurus* (right) 7.6 mm SL and *C. equiselis* (left) 7.6 mm SL. Symbols: Eps, epurals; Hs, haemal spine; Hy, hypural; "Na", specialized neural arch; Ns, neural spine; Ph, parhypural; Pu, preural centrum; Un, uroneural; Ur, urostyle. Stippled, cartilage; darkened, ossifying bones; stippled darkened areas are cartilage just beginning to ossify.

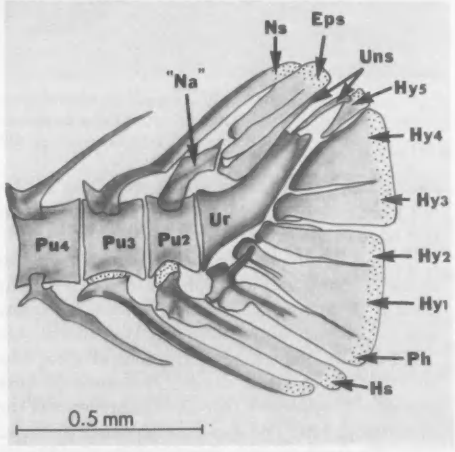


FIGURE 20.—Supporting bones of the caudal complex of *Coryphaena equiselis*, 11.0 mm SL. Symbols: Uns, uroneurals. For explanation of other symbols, see Figure 19. Stippled, articular cartilage; darkened, bone.

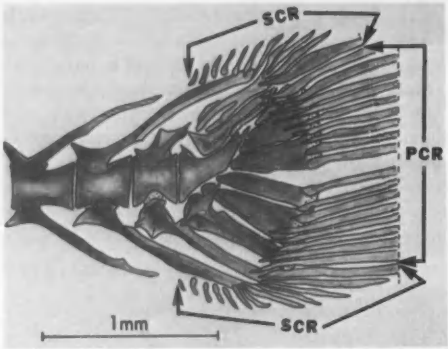


FIGURE 21.—Caudal complex of *Coryphaena equiselis*, 15.9 mm SL. Symbols: PCR, principal caudal rays; SCR, secondary caudal rays. Stippled, articular cartilage; darkened, bone.

autogenous (Figures 23, 24). These were two haemal spines, a parhypural, a ventral and dorsal hypural plate, hypural 5, a uroneural pair (fused from two pairs), and an epural (fused from two). Nonautogenous bones were the specialized neural arch and one neural spine. The relationship of the urostyle with the uroneural pair and hypural 5 is shown in Figure 24. Articular cartilage was present on all distal parts of the hypural complex posterior to preural centrum 4 (Figure 22).

The parhypural and hypurals 1-5 supported the principal caudal rays. The distribution of principal caudal rays on the various hypural bones can only be seen in larvae and smaller juveniles of both species before hypural fusion (Table 11). There was no difference in distribution of principal caudal rays between the two species.

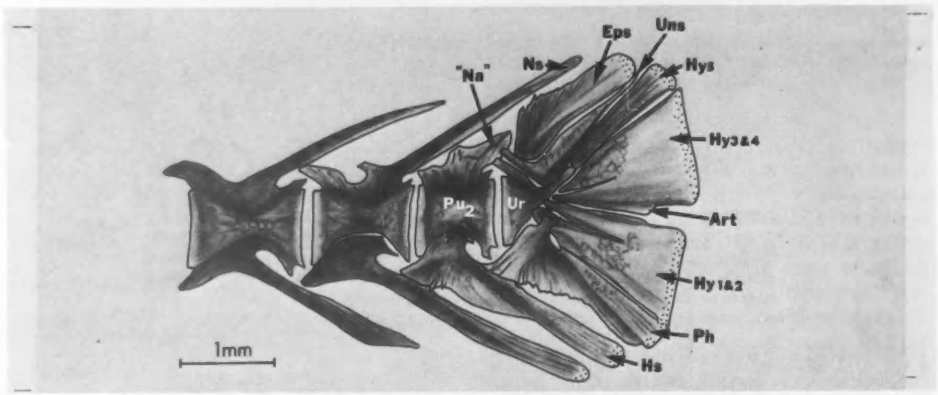


FIGURE 22.—Supporting bones of the caudal complex of *Coryphaena equiselis*, 55.5 mm SL. Symbols: Art, articular projection. For explanation of other symbols, see Figures 19, 20. Stippled, articular cartilage; darkened, bone.

phaena spp. remained autogenous in the adults, but were closely articulated with the ventroposterior edge of the urostyle.

During development of the hypural complex bones a small hypurapophysis (Lundberg and Baskin 1969) was observed on hypural 1 in both species. It appeared before hypural fusion, but could not be illustrated in the lateral view. Disarticulation of adult caudal skeletons of both species of *Coryphaena* revealed the presence of the hypurapophysis. The hypurapophysis articulated with the urostyle just dorsad of the parhypurapophysis (Nursall 1963).

In the adults of *Coryphaena* spp., most bones of the hypural complex were closely articulated, but

The anatomy and development of the caudal complex of *Coryphaena* spp. had similarities and dissimilarities with other fish. The hypurapophysis observed in *Coryphaena* spp. was noted in such fish as siluriform catfish (Lundberg and Baskin 1969) and adult sea bream, *Archosargus rhomboidalis* (Houde and Potthoff 1976). The hypurapophysis was not observed in the blackfin tuna, *Thunnus atlanticus* (Potthoff 1975).

In the Coryphaenidae and other percoid fishes such as Apogonidae (Fraser 1972), *A. rhomboidalis* (Houde and Potthoff 1976), Carangidae (Ahlstrom and Ball 1954; Berry 1969), *Haemulon plumieri* (Saksena and Richards 1975), and some Scombridae (Conrad 1938; Mago Leccia 1958), the

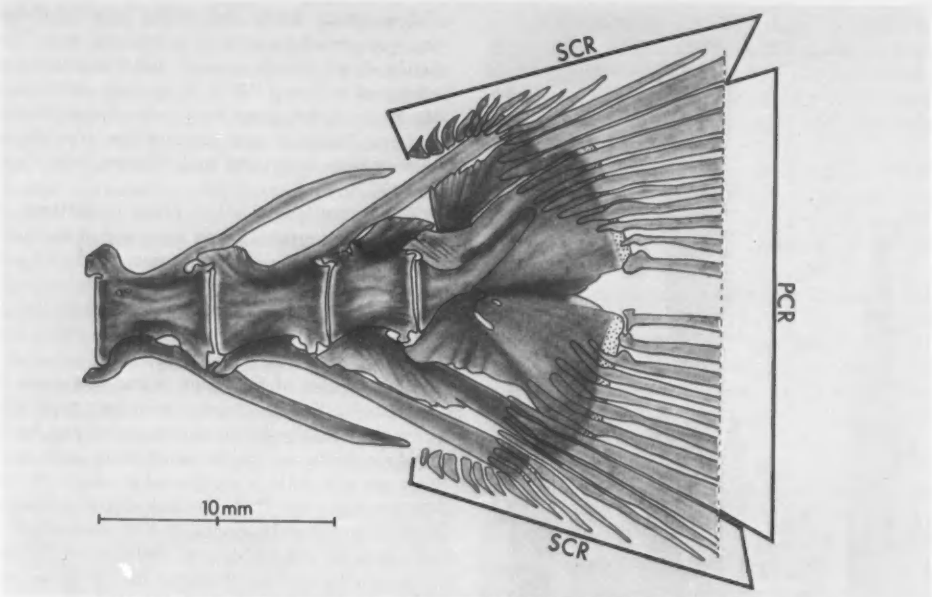


FIGURE 23.—Caudal complex of a *Coryphaena equiselis*, 230 mm SL. For explanation of symbols, see Figure 21. Stippled, articular cartilage; darkened, bone.

TABLE 11.—Distribution of principal caudal rays on the hypurals in 135 *Coryphaena hippurus* (8.0-53 mm SL) (*C. h.*) and 75 *C. equiselis* (7.0-52 mm SL) (*C. e.*).

	Number of principal caudal rays									
	1		2		3		4		5	
Part	*C. h.*	*C. e.*	*C. h.*	*C. e.*	*C. h.*	*C. e.*	*C. h.*	*C. e.*	*C. h.*	*C. e.*
Parhypural			51	24	85	51				
Hypural 1					52	22	80	51	4	2
Hypural 2	39	32	97	43						
Hypural 3			28	27	97	45	11	3		
Hypural 4					6		72	36	58	39
Hypural 5	37	16	98	58	1	1				

epurals were autogenous. In part of the Scombridae (Fierstine and Walters 1968; Monod 1968; Patterson 1968; Collette and Chao 1975; Potthoff 1975) the anteriormost epural is secondarily fused to the specialized neural arch of preural centrum 2. Based on the epurals, *Coryphaena* spp. is advanced because epural numbers are reduced from 3 to 2 and fused to 1 (Patterson 1968; Fraser 1972).

The haemal spines of preural centrum 2 and 3 were autogenous in *Coryphaena* spp. This state is considered basic because advanced percoids have these spines secondarily fused to the centra (Fraser 1972). Fusion of these haemal spines occurs in *T. atlanticus* (Potthoff 1975), and some apogonids (Fraser 1972).

The two prezygapophyses of the urostyle (Figure 24) of *Coryphaena* spp. are true prezygapophyses; whereas in *T. atlanticus* and other Thunnini and Sardini (Collette and Chao 1975; Potthoff 1975) the prezygapophyses of the urostyle represent the pair of uroneurals which have fused to the urostyle during development.

Articular cartilage was present in *Coryphaena* spp. on the caudal complex on all parts distally inclusive of preural centrum 3. No articular cartilage was observed anterior to this centrum. Articular cartilage was observed in scombrids by Fierstine and Walters (1968), in *T. atlanticus* by Potthoff (1975), and in *A. rhomboidalis* by Houde and Potthoff (1975). The absence of articular cartilage in the caudal complex drawings of

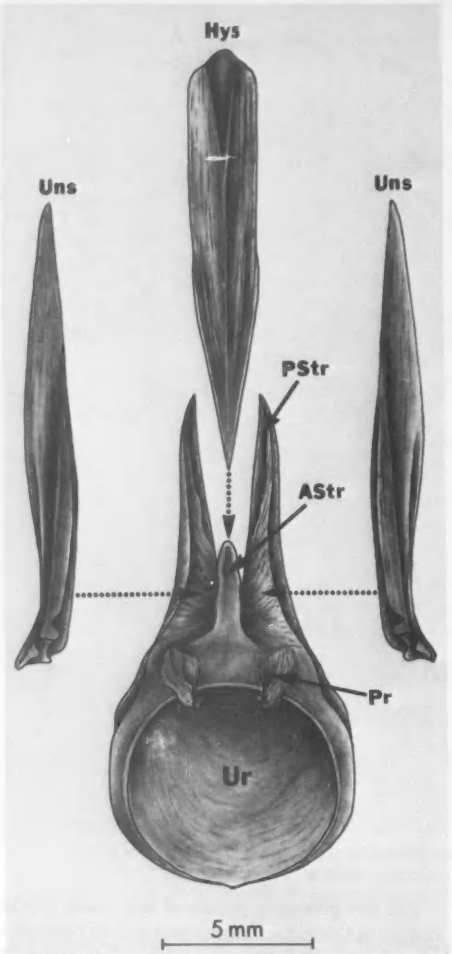


FIGURE 24.—Urostyle of a *Coryphaena equiselis*, 330 mm SL, with disarticulated uroneurals and hypural 5. Dashed lines with arrows point towards place of articulation. Symbols: AStr, anterior strut of urostyle; Hy, hypural; Pr, prezygapophysis; PStr, posterior strut of urostyle; Uns, uroneurals; Ur, urostyle. The articular cartilage is not shown on hypural 5 because of the boiling and drying method of preparation.

apogonids (Fraser 1972) is probably an oversight by the author since he used cleared and stained material. The lack of articular cartilage in most of the drawings of caudal complexes by Monod (1968) can probably be attributed to the method of skeletal preparation, e.g., boiling and subsequent drying.

Autogenous dorsal and ventral hypural plates were observed in adult *Coryphaena* spp. The fusion of individual hypural bones was considered advanced by Fraser (1972). Even more advanced is the fusion of all hypural bones to one hypural plate and the fusion of this plate to the urostyle as in scombrids (Fierstine and Walters 1968; Potthoff 1975).

The formation of articulatory projections of membranous origin during ontogeny at the midline of the caudal complex between the dorsal and ventral hypural plates was observed in *Coryphaena* spp. (Figures 20-22) as well as in *Scombrolabrax heterolepis* (Potthoff et al. 1980), but not in *T. atlanticus* (Potthoff 1975).

Both species of *Coryphaena* had two pairs of uroneurals. The smaller posterior pair gradually moved anteriorly during development and fused to the outsides of the larger anterior pair, until only one pair could be recognized in adults. Fraser (1972) contended that the loss of the posterior pair of uroneurals constituted an evolutionary advance. He did not completely rule out fusion, although he had no evidence for it. There are fishes such as the scombrids which only develop one pair of uroneurals (Potthoff 1975). Loss or fusion of uroneurals can be ascertained through the examination of developmental series.

Pectoral Fin and Supports

The following description is based upon juveniles >13 mm SL of both *Coryphaena* species with adult counts of 19-21 rays. These counts were obtained between 19 and 13 mm SL in *C. equiselis* and between 11 and 13 mm SL in *C. hippurus*. Individual differences in counts between the left and right pectoral fins were lower in both species of *Coryphaena* than in four species of *Thunnus* (Potthoff 1974). Only 1% of 171 *Coryphaena* spp. examined with adult counts >13 mm SL differed by 2 rays between each side, 18% differed by 1 ray, and 81% had the same count on both sides. The pectoral fin rays were directly and indirectly supported on each side by a number of bones which composed the pectoral girdle and its suspensorium. On each side the pectoral girdle consisted of a scapula (which supported the first fin ray directly), four radials (which supported the remainder of the rays directly), a coracoid, and a cleithrum. The scapula and coracoid were connected by cartilage. The suspensorium consisted of seven bones. The supracleithrum and posttemporal were attached

in a row from the outside of the posterior plate of the cleithrum to the rear of the skull and postcleithra 1 and 2 extended over the abdominal area from the inside of the posterior process of the cleithrum. The supratemporal and two intertemporals, which belong with the posttemporal to the laterosensory canal (Harrington 1955), originated just anterior to the posttemporal and ended just short of the supraoccipital crest. Except for individual variation there was no specific difference in the shape of bones of the girdle and suspensorium between the two species. The relationship of bones of the pectoral girdle, suspensorium, and pelvic basipterygium to each other is shown in Figure 25.

Formation of the pectoral fin rays started in the dorsal border of the larval pectoral blade (Figure 26) and continued ventrad (Figure 27). For equal-sized specimens from 6.5 to 13 mm SL, *C. equiselis* had more pectoral fin rays than *C. hippurus* (Figure 28). Of 86 individuals of both species with developing fins <13 mm SL, 5% differed by 2 rays between the left and right sides, 43% differed by 1 ray between the sides, and 52% had the same count on both sides.

The two species differed in length at which development of the pectoral girdle occurred but not in its structure (Table 12). The 6.5 mm NL *C. equiselis* had the same pectoral girdle development as a 6.5 mm NL *C. hippurus*. For individuals of equal length between 7.6 and 18 mm SL, *C. equiselis* was more advanced. At lengths >18 mm SL specimens of both species had the pectoral girdle equally developed except for the supratemporal-intertemporal bones which were first seen at 13 mm SL in *C. equiselis* and at 18 mm SL in *C. hippurus*.

Regarding development of the pectoral girdle in *C. hippurus*, the smallest (5 mm NL) specimen had a simple rod-shaped, bony cleithrum, and a coraco-scapular cartilage (Figure 26). The car-

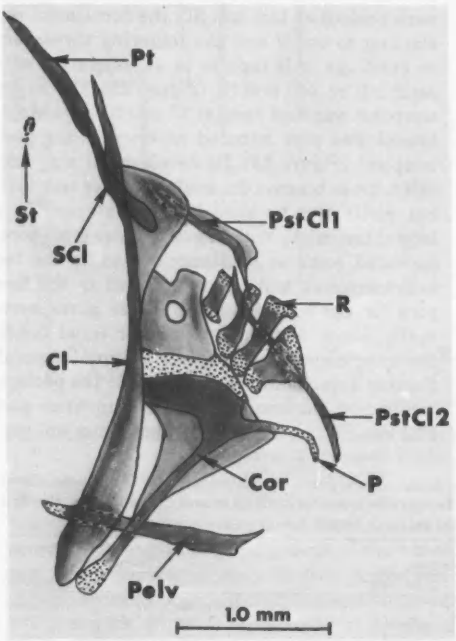


FIGURE 25.—Lateral external view of left sides of pectoral girdle and suspensorium from a 20.8 mm SL *Coryphaena hippurus*. Symbols: Cl, cleithrum; Cor, coracoid; P, posterior process of the coraco-scapular cartilage; Pelv, pelvic basipterygium; PstCl 1, postcleithrum 1; PstCl 2, postcleithrum 2; Pt, posttemporal; R, radial; SCl, supracleithrum; St, supratemporal (beginning to develop). Stippled, cartilage; darkened, bone.

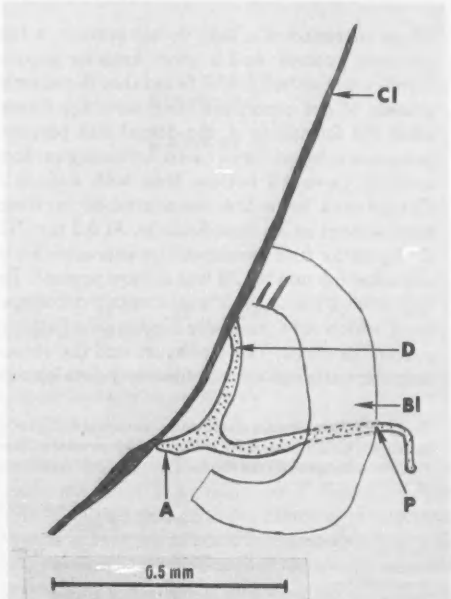


FIGURE 26.—Lateral external view of left side of pectoral girdle from a 5.0 mm NL *Coryphaena hippurus*. Symbols: A, anterior process of the coraco-scapular cartilage; Bl, blade of the larval pectoral fin with two fin rays developing dorsally; Cl, cleithrum; D, dorsal process of the coraco-scapular cartilage; P, posterior process of the coraco-scapular cartilage. Stippled, cartilage; darkened, bone.

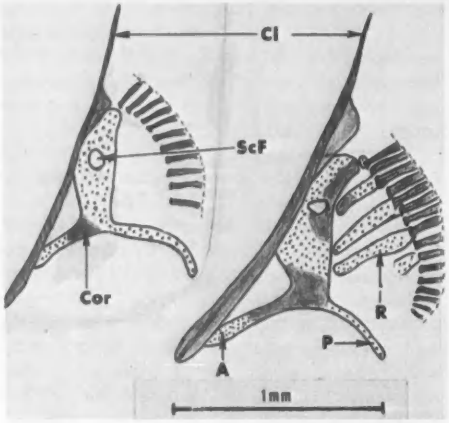


FIGURE 27.—Lateral external view of left side of pectoral girdle from a 8.1 mm SL *Coryphaena hippurus* (left) and a 7.9 mm SL *C. equiselis* (right). Symbols: ScF, scapular foramen. For explanation of other symbols, see Figures 25, 26. Stippled, cartilage; darkened, bone.

tilage consisted of a long dorsal process, a long posterior process, and a short anterior process. Houde and Potthoff (1976) found that the anterior process of the coraco-scapular cartilage formed after the formation of the dorsal and posterior processes in laboratory-reared *Archosargus rhomboidalis* larvae. I believe that both species of *Coryphaena* have the same kind of cartilage development as *A. rhomboidalis*. At 5.5 mm NL, *C. hippurus* first developed the supracleithrum, and after 6.3 mm NL, it was always present. The supracleithrum at first was a small rod-shaped bone, which only gradually acquired its flattened paddlelike shape. The cleithrum and the coraco-scapular cartilage did not show any development between 5 and 7.3 mm NL. The posttemporal first developed as a small, rod-shaped bone at 6.3 mm NL. In larvae of 7.4 mm SL the scapular foramen was first seen in the dorsal process of the coraco-scapular cartilage, and at 7.6 mm SL the posterior process of the cleithrum first appeared (Figure 27). Between 7.6 and 8.4 mm SL many developmental changes occurred. In an 8 mm SL specimen the first dorsalmost radial was seen in cartilage; the radial was absent in an 8.1 mm SL specimen (Figure 27), but present again at 8.3 mm SL. The bony rod-shaped postcleithrum 2 was first seen at 8.3 mm SL. Ossification of the coraco-scapular cartilage started at 8.1 mm SL in the region of the future coracoid at the juncture of the dorsal and anterior processes. The scapula started to ossify first around the scapular foramen at 9.5 mm SL. Also at 9.5 mm SL the postcleithrum 1 was first seen as a tiny speck of bone, but not until 11.9 mm SL was this structure easy to see. All four radials were present at 11.9 mm SL; the dorsalmost was starting to ossify and the following three were in cartilage. All radials in *C. hippurus* were ossifying by 12.3 mm SL (Figure 29). The supratemporal was first seen at 18 mm SL as a single lateral line pore situated anterior to the posttemporal (Figure 25). Its development was difficult to trace because the adult bone was very thin, but distinctive because it was traversed by a lateral line canal. With increasing size more pores appeared, some at a distance dorsad for the two intertemporals and others adjacent to the first pore for the supratemporal. These pores eventually joined to form two tubular canal bones, the intertemporals and the thin supratemporal. Further development of the bones in the pectoral girdle and suspensorium of *C. hippurus* past 12.3 mm SL (when all component bones are ossi-

TABLE 12.—Development of structures, bones and fin rays of the pelvic and pectoral girdles for the two species of *Coryphaena*, shown for lengths (in millimeters NL or SL) at which structures, bones or fin rays first appear in cartilage or ossify. Lengths given signify a first observance and do not necessarily apply to all specimens of that length or longer.

Part	First appearance in cartilage		First evidence of ossification (Stain uptake)	
	C. hippurus	*C. equiselis*	*C. hippurus*	*C. equiselis*
Cleithrum	—	—	not known	not known
Scapula	not known	not known	9.5	7.0
Scapular foramen	7.4	7.0	—	—
Coracoid	not known	not known	8.1	7.0
Radials 1-4	8.0-11.9	8.0-8.9	11.9-12.3	8.8- 9.8
Posttemporal	—	—	6.3	not known
Supracleithrum	—	—	5.5	not known
Postcleithrum 1	—	—	9.5	8.9
Postcleithrum 2	—	—	8.3	7.4
Supratemporal-intertemporals	—	—	18.0	13.0
Pectoral fin rays	—	—	5.0	not known
Pelvic basipterygium	7.0	(6.0?) 7.0	8.7	8.7
Pelvic fin rays	—	—	7.0	7.3

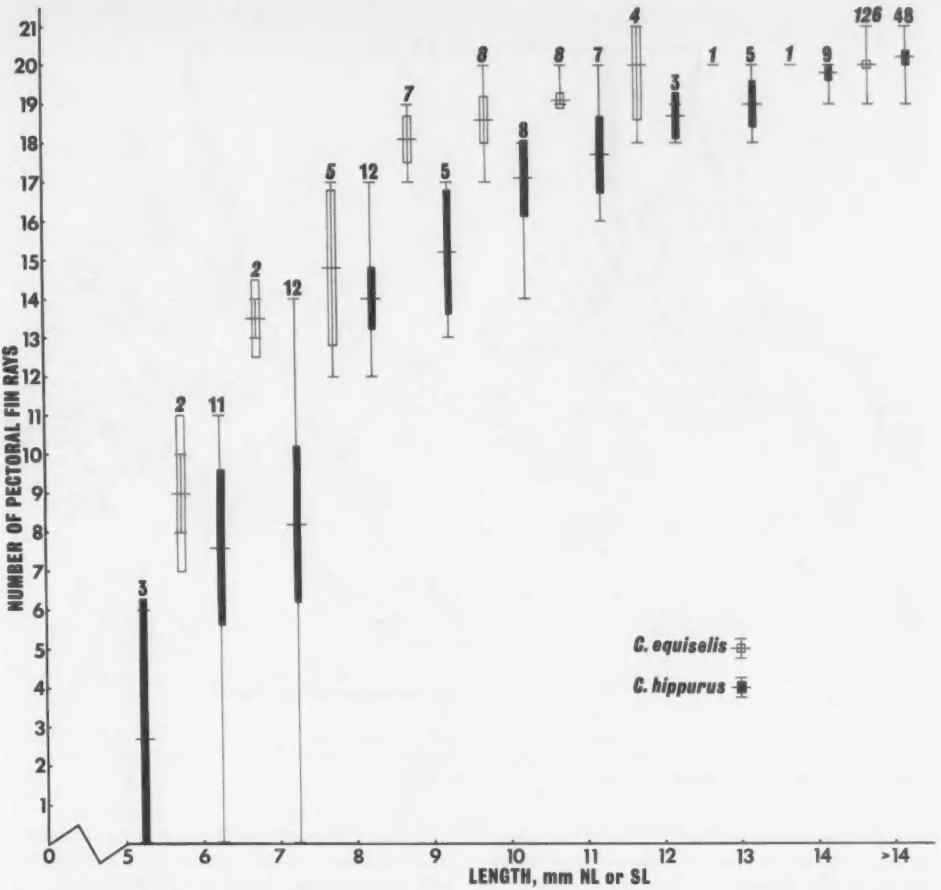


FIGURE 28.—Number of left pectoral fin rays in relation to length in 164 *Coryphaena equiselis* (6.5-230 mm NL or SL) and 123 *C. hippurus* (5-172 mm NL or SL). For explanation of symbols, see Figure 1.

fying, except the supratemporal-intertemporals) consisted of ossification and growth of the bones, and the formation of bony shelves on the cleithrum, coracoid, posttemporal, and postcleithrum 1 (Figures 29, 30). The supratemporal developed thin membranous bones around the lateral line canal tubes. Development also involved loss of cartilage. The cartilage separating the scapula and coracoid became narrower with increasing length (Figures 29, 30). The cartilage from the prominent larval posterior process of the coracoid completely disappeared by 40 mm SL (Figure 30).

No developmental studies of the pectoral fin and supports have been done for *Coryphaena* spp. Starks (1930) studied the anatomy of the pectoral girdle in a variety of adult bony fishes including *C. hippurus*. The development of the coraco-scapular cartilage to a scapula and a coracoid bone and some or total atrophy of the cartilaginous posterior process of the coracoid occurs in most fishes (Swinnerton 1905; Starks 1930). More recently Houde and Potthoff (1976) observed the atrophy of the posterior process in *A. rhomboidalis* and Saksena and Richards (1975) reported the presence

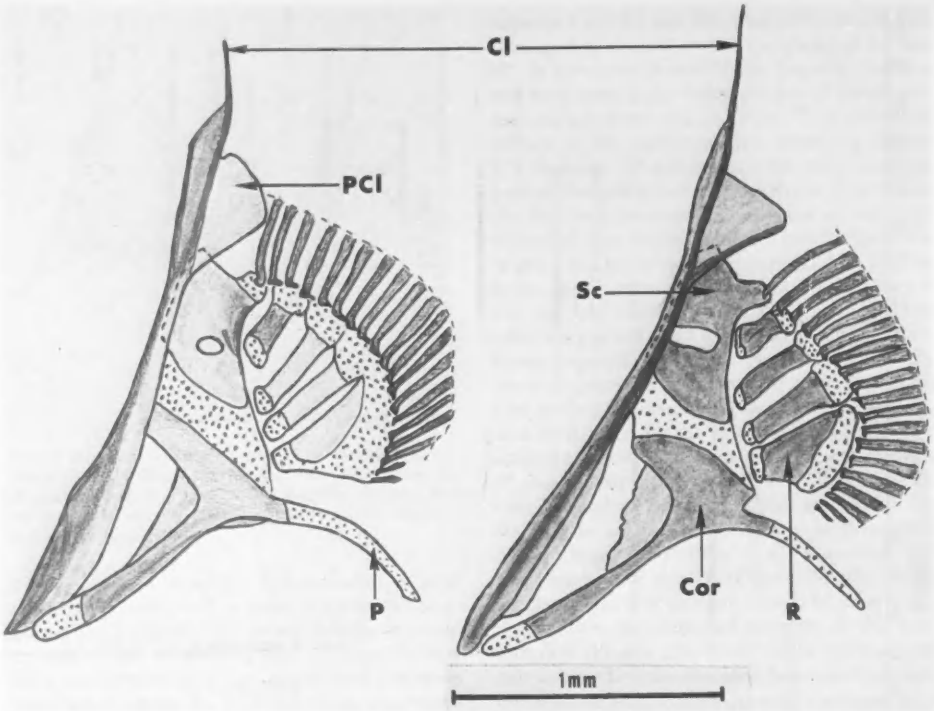


FIGURE 29.—Lateral external view of left side of pectoral girdle from a 12.3 mm SL *Coryphaena hippurus* (left) and a 10.3 mm SL *C. equiselis* (right). Symbols: Cl, cleithrum; Cor, coracoid; P, posterior process of the coraco-scapular cartilage; PCl, posterior process of the cleithrum; R, radial; Sc, scapula. Stippled, cartilage; darkened, bone.

of a Y-shaped cartilaginous coracoid (probably coraco-scapular cartilage) in *Haemulon plumieri* larvae. In the Blenniidae, Characidae, and Pholidichthyidae, a small posterior process of the coracoid was observed in adults (Weitzman 1962; Springer 1968; Springer and Freihofer 1976). For the family Gobiesocidae, however, Springer and Fraser (1976) reported large posterior processes of the coracoid. Thus, it seems that the posterior process of the coracoid is present in most fishes, but that it disappears during development in more advanced forms. It also appears that this process remains as a neotenic structure in small fishes.

In more primitive fishes such as the Osteoglossidae (Greenwood and Thomson 1960), Characidae (Weitzman 1962), most stomiatoid families (Weitzman 1974), and *Lile piquitinga* (Clupeidae) (Gomez Gaspar 1976) a mesocoracoid was present. This bone is absent in the Coryphaenidae.

The presence of intertemporals is considered primitive because these bones are absent in more advanced groups, such as scombrids (Collette and Chao 1975).

Pelvic Fin and Fin Supports

Description is based on large juveniles of both species >90 mm SL, two adults of *C. equiselis* and two adults of *C. hippurus*. There were I,5 rays in each of the pelvic fins which were located on the underside of the body below the pectoral fin. All *C. hippurus* >10.7 mm SL and all *C. equiselis* >8.6 mm SL had the full count. Each side of the pelvic fin was supported by a basipterygium; no radials were present. The two basipterygia were closely approximated medially, but not fused (Figure 31). They were located in the abdominal body wall and were lying between the ventral portions

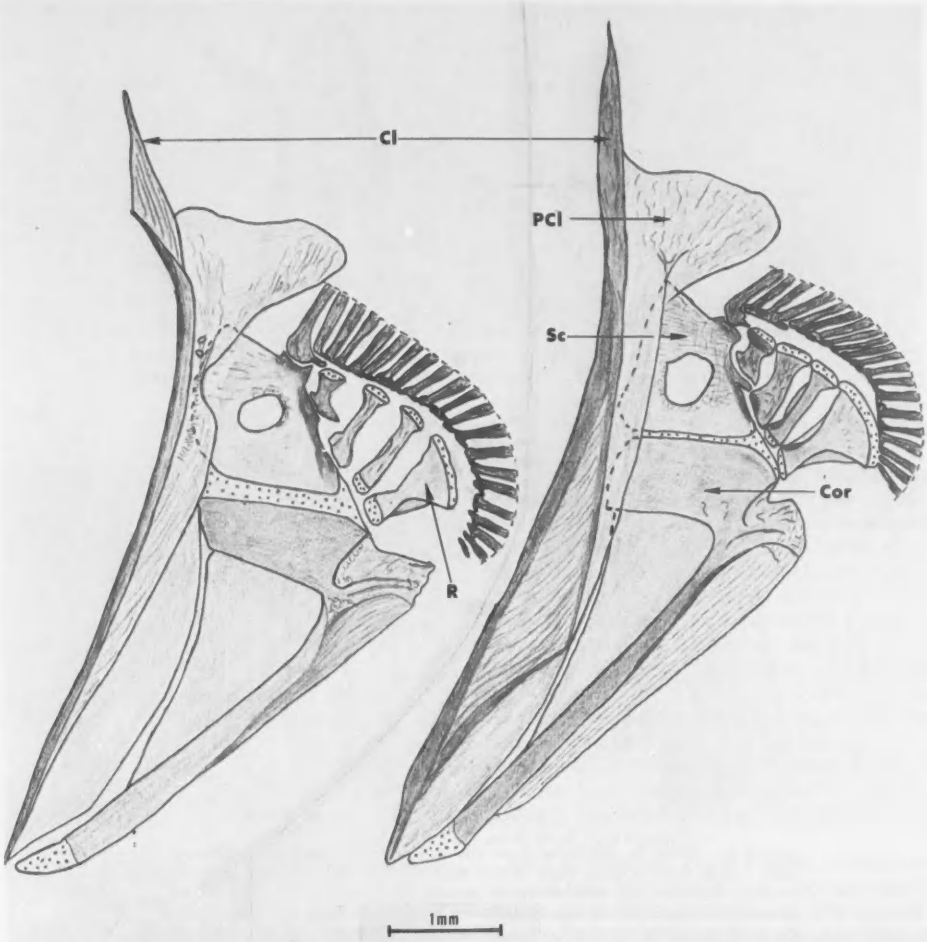


FIGURE 30.—Lateral external view of left side of pectoral girdle from a 47.6 mm SL *Coryphaena hippurus* (left) and a 48 mm SL *C. equiselis* (right). For explanation of symbols, see Figure 29. Stippled, cartilage; darkened, bone.

of the two cleithra and coracoids (Figure 25). No fleshy interpelvic processes were present between the bases of the fins.

The basipterygium is a complex bone. For convenience of description, it was divided into three parts which corresponded to the ontogeny of the bone: the central part, which was the original cartilage, the wings (Kishinouye 1923) of membranous bone origin, and the two xiphoid processes (de Sylva 1955), of which the posterior process was of cartilage origin and the anterior process of bone origin. The central part of the basipterygium carried the four wings along its length (Figures 31-33). Anteriorly the central part was tipped by a small piece of cartilage. Posteriorly the central part served the articulation of the fin rays. A thin layer of articular cartilage was present in adults on the posteriormost portion of the central part (Figures 31, 32). Each basipterygium had four wings, reminiscent of the two sagittal and two lateral keels of pterygiophores. The wings formed a dorsal and a ventral "V" shaped groove, and a

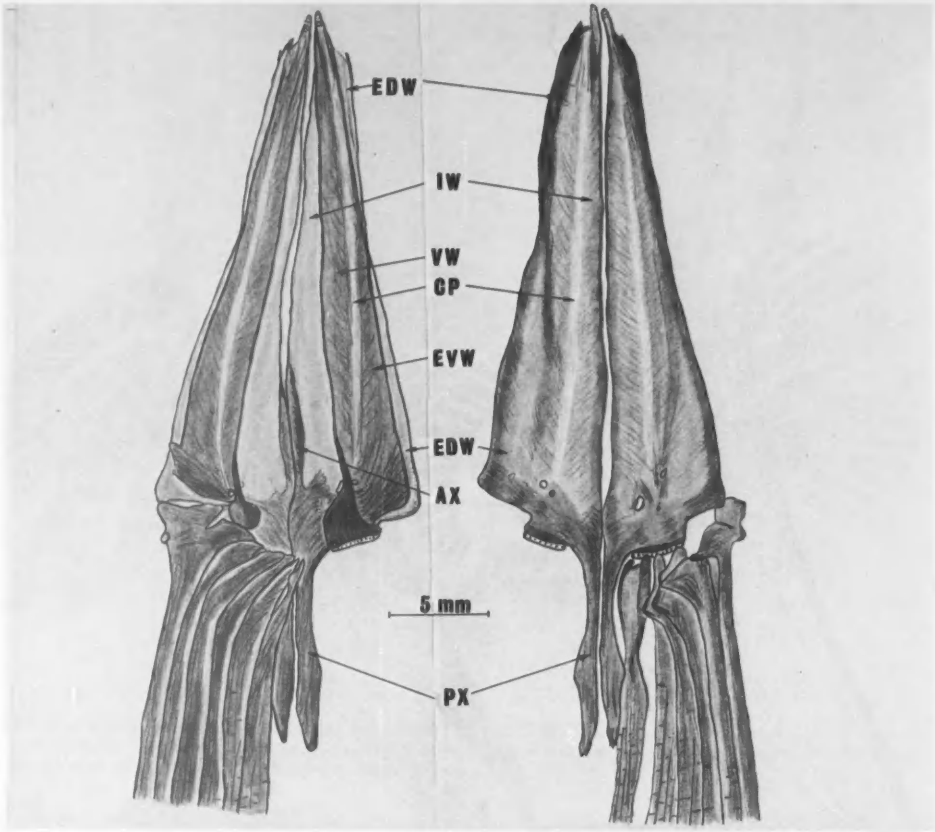


FIGURE 31.—Pelvic fin and basipterygia from a 449 mm SL *Coryphaena hippurus*. Left: ventral external view; right: dorsal internal view. Left pelvic fin has been removed. Symbols: AX, anterior xiphoid process; CP, central part; EDW, external dorsolateral wing; EVW, external ventrolateral wing; IW, internal dorsolateral wing; PX, posterior xiphoid process; VW, ventral wing. Stippled, cartilage; darkened, bone.

lateral "[" shaped channel (Figure 33). The xiphoid processes were located internally at the midline on the basipterygia (Figures 31-33). The anterior xiphoid process was an anteroventral extension of the posterior xiphoid process (Figure 32). The posterior xiphoid process, which pointed in a posterodorsal direction was attached to the posterior part of the basipterygium by a heavy bony strut from the central part and anteriorly by the internal dorsolateral wing (Figures 32, 33). The two basipterygia were closely approximated at the edges of the two internal dorsolateral wings and the internal surfaces of the four xiphoid processes (Figure 31). The closest approximation was observed on the xiphoid processes at the place where the anterior and posterior processes were joined (Figure 32). Here the bone was rough with minute projections. These projections gave a close fit when the surfaces were brought together and prevented the basipterygia from sliding.

No anatomical differences in the development of the pelvic fin and supports were found between *C. hippurus* and *C. equiselis*. Larval and juvenile specimens of *C. equiselis* were more advanced in pelvic development than equal-sized specimens of *C. hippurus* (Table 13; Figures 34, 35). In both

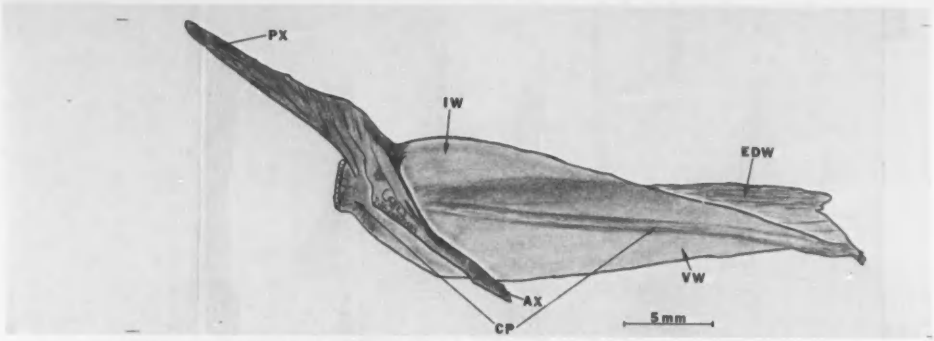


FIGURE 32.—Lateral internal view of left basipterygium from a 449 mm SL *Coryphaena hippurus*. For explanation of symbols, see Figure 31. Stippled, cartilage; darkened, bone.

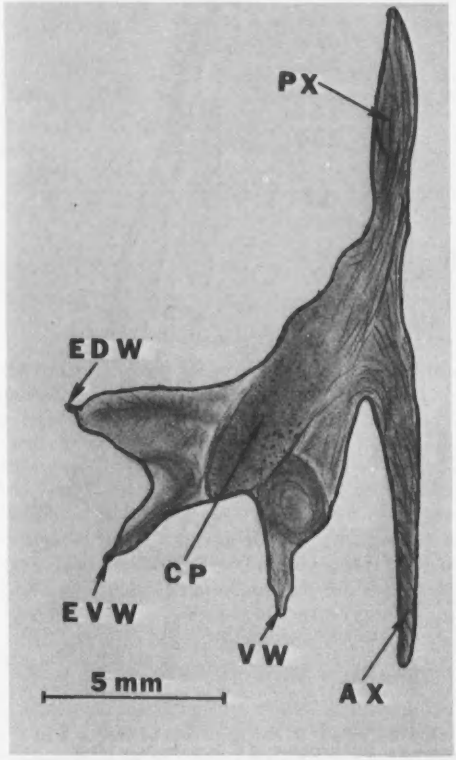


FIGURE 33.—Posterior view of left basipterygium after left pelvic fin had been removed from a 449 mm SL *Coryphaena hippurus*. For explanation of symbols, see Figure 31.

species a fin bud developed first on the abdomen (Table 13). Simultaneously to the fin bud appearance, two cartilaginous basipterygia developed internally at 7 mm SL in flexion larvae of *C. hippurus*. In *C. equiselis* it probably occurred in flexion larvae between 6 and 7 mm SL, but the smallest available specimen measured 7 mm SL (Table 12). The pelvic fin rays developed in the fin bud after basipterygium formation. Fin ray appearance was from the outside of the specimen towards its midline in both species, so that the first ray to appear was the spinous ray. In *C. hippurus* the pelvic fin ray development began at 7-7.5 mm SL and was completed at 10.7 mm SL, and in *C. equiselis* it began at 7.3 mm SL and was completed at 8.6 mm SL.

Each cartilaginous basipterygium in both species was cylindrical with its base expanded posteriorly near the fin bud (Figure 34). The cartilaginous projection of the posterior xiphoid process developed posteriorly at the inner corner of the expanded base (Figure 34). Ossification of the basipterygium cartilage to the central part began in both species at the center and progressed anteriorly and posteriorly as the larvae grew (Figure 34). For *C. hippurus* it began at 8.7-10.8 mm SL, and for *C. equiselis* at 8.7 mm SL (Tables 12, 13). After the cartilaginous central part of the basipterygium had ossified, all structures of membranous origin developed simultaneously; these were the anterior xiphoid process and the four wings (Figure 34). All wings developed from the base in an anterior direction. The posterior xiphoid process was of cartilage origin and started

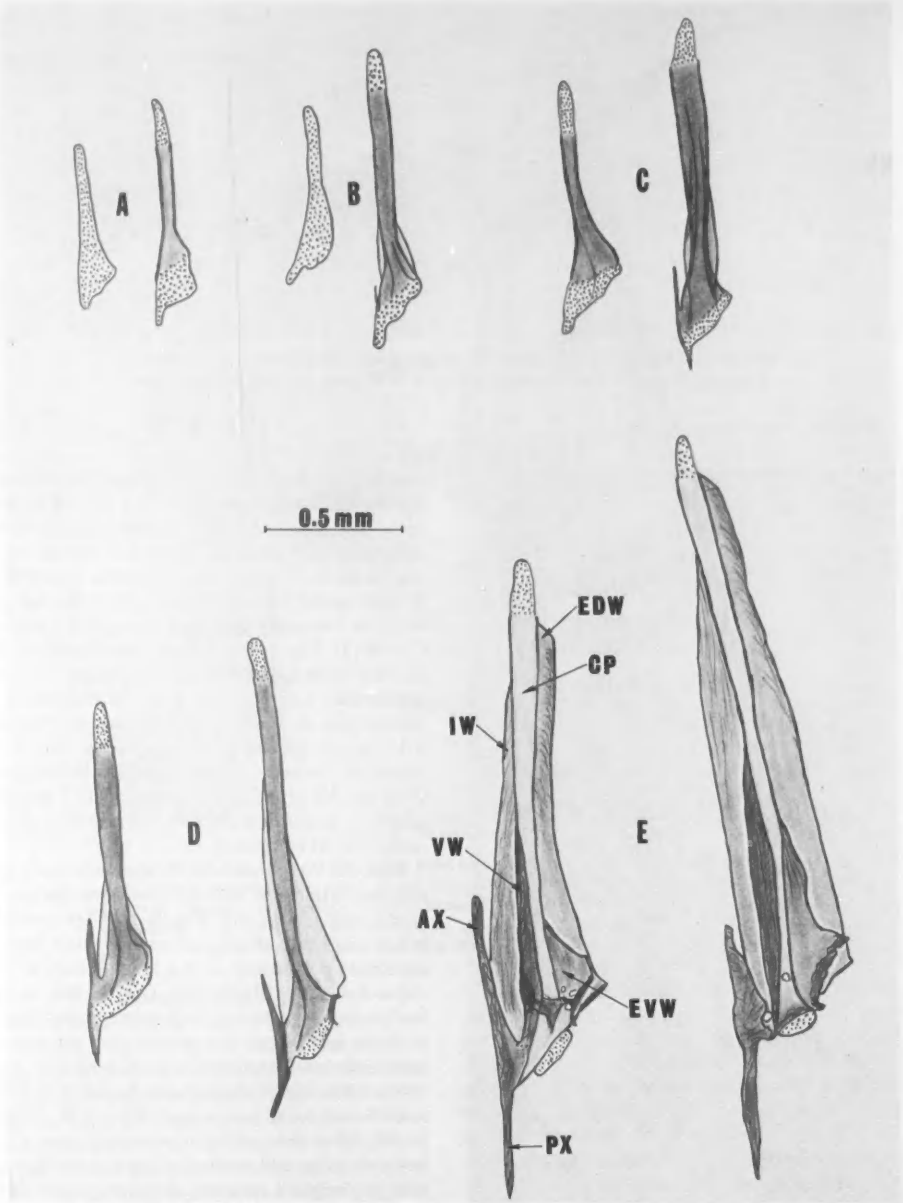


FIGURE 34.—Development of left basipterygium of *Coryphaena* spp. Basipterygium of *C. hippurus* is to left of letters, that of *C. equiselis* is to right. Lengths: A, 8.3 and 8.9 mm SL; B, 10.3 and 10.1 mm SL; C, both 11.3 mm SL; D, 14.1 and 14.2 mm SL; E, 21 and 20.9 mm SL. For explanation of symbols, see Figure 31. Stippled, cartilage; darkened, bone.

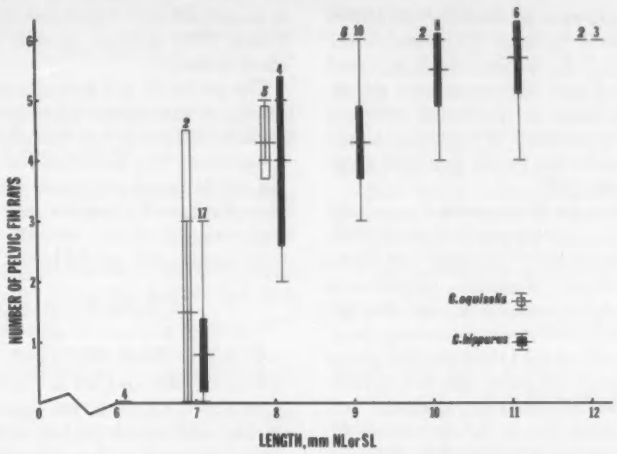


FIGURE 35.—Number of pelvic fin rays in relation to length in 15 *Coryphaena equiselis* (7.0-12.4 mm SL) and 52 *C. hippurus* (6.0-12.5 mm NL or SL). For explanation of symbols, see Figure 1.

TABLE 13.—Development of pelvic fin and supports in 52 *Coryphaena hippurus* (6.0 mm NL-12.5 mm SL) (*C. h.*) and 15 *C. equiselis* (7.0-12.4 mm SL) (*C. e.*). Numbers denote number of specimens, dashes denote specimens not available.

Length mm NL or SL	Fin bud				Fin rays				Basipterygia					
	Absent		Present		Absent		Present		Absent		Cartilaginous		Ossifying	
	C. h.	*C. e.*	*C. h.*	*C. e.*	*C. h.*	*C. e.*	*C. h.*	*C. e.*	*C. h.*	*C. e.*	*C. h.*	*C. e.*	*C. h.*	*C. e.*
5.6- 6.5	4	—	0	—	4	—	0	—	4	—	0	—	0	—
6.6- 7.5	6	0	11	2	12	1	5	1	10	0	7	2	0	0
7.6- 8.5	0	0	4	3	0	0	4	3	0	0	4	3	0	0
8.6- 9.5	0	0	10	6	0	0	10	6	0	0	9	0	1	6
9.6-10.5	0	0	8	2	0	0	8	2	0	0	1	0	7	2
10.6-11.5	0	—	6	—	0	—	6	—	0	—	1	—	5	—
11.6-12.5	0	0	3	2	0	0	3	2	0	0	0	0	3	2

to ossify shortly after the appearance of the anterior xiphoid process (Figure 34).

A comparison of pelvic bones of *Coryphaena* spp. with those of more primitive fishes revealed the absence of radials in *Coryphaena* spp. It is not known if the radials have been lost, or if they have fused to the central part and the articular cartilage during evolution. In the more primitive stomiatoid fish families (Weitzman 1974) and in *Lile piquitinga* (Gomez Gaspar 1976), radials are present between the bases of the fin rays.

DISCUSSION

In a tentative classification of the Perciformes, Greenwood et al. (1966) placed the Coryphaenidae to follow the family Carangidae. This placement was arbitrary because *Coryphaena* spp. is more advanced than some families that follow in the placement.

The one continuous dorsal fin of *Coryphaena* spp. extends to the head, so that the first interneural space, bounded by the head bones and the first neural spine, is occupied by pterygiophores which support the fin rays. Smith and Bailey (1961) contended that the dorsal fin of *Coryphaena* spp. represents an evolutionary advance and specialization because of its anterior extension and the loss or reoccupation by fin rays of the predorsal bones. In diverse fishes, such as characins, sparids, carangids, scombrids, and lutjanids, the pterygiophores in the posterior parts of the dorsal and anal fins have three parts. This triserial pterygiophore structure is considered basic (Eaton 1945; Lindsey 1955; Johnson 1978). Most pterygiophores in *Coryphaena* spp. are biserial, and one or two anteriormost ones uniserial. Thus, the pterygiophores of

Coryphaena spp. are more advanced or specialized due to either a loss or fusion of the middle radial. The loss of the "stay" for the posteriormost dorsal and anal pterygiophore also represents an advance. Therefore, based on the dorsal and anal fin and supports, placement of *Coryphaena* spp. should be phylogenetically higher than that given by Greenwood et al. (1966).

The vertebral number is higher for *C. equiselis* than for *C. hippurus* (Jordan and Evermann 1896; Collette et al. 1969), yet *C. equiselis* has fewer dorsal fin rays than *C. hippurus*. *Coryphaena equiselis* also tends to have fewer anal fin rays than *C. hippurus*. Therefore, since fin ray number is approximately equal to the pterygiophore number, *C. equiselis* has fewer dorsal pterygiophores arranged in more interneural spaces, and *C. hippurus* has more dorsal pterygiophores arranged in fewer interneural spaces. The situation is similar for the anal fin. It is noteworthy that the same number of vertebrae is found in both species posteriorly to the end of the dorsal and anal fins (Figure 3). The evolutionary significance of the relationship between vertebral numbers and pterygiophore numbers is not understood (Lindsey 1955), but may be phylogenetically important.

During development, except for the presence of two rather than three epurals, *Coryphaena* spp. have the basic (unreduced) perciform caudal skeleton (Gosline 1961a; Monod 1968; Patterson 1968; Fraser 1972). Adults of *Coryphaena* spp., however, have a more advanced caudal skeleton. The presence of a single epural and uroneural, as well as a dorsal and ventral hypural plate, shows advance over the basic type, although the fused parts remain autogenous. In the modified and advanced caudal complex of most Scombridae these parts may be fused to the centra. For example, the epural may be fused to the specialized neural arch, the uroneurals and hypural plates may be fused to the urostyle, the parhypural and the hypural plate may be fused to the urostyle, and two haemal spines may be fused to preural centra 2 and 3.

The pectoral skeletons of *Coryphaena* spp. are of the basic perciform type. The pectoral supports fit the description of Greenwood et al. (1966) for the Acanthopterygii. The presence of supratemporal-intertemporal bones and two postcleithra in *Coryphaena* spp. characterize them as a basic perciform pectoral support system. Some fishes may lose some or all supratemporal-intertemporal bones (Scombridae) and some also may lose a postcleithrum (*Gymnapogon*, Apogonidae, Fraser 1972; *Xiphias gladius*, author's personal observation).

The pelvic fin and supports are of the acanthopterygian (perciform) type, one bone supporting an unbranched and five branched rays in a thoracic position. The development and structure of the pelvic basipterygium is similar to that of a pterygiophore. The central part and wings of the basipterygium closely resemble proximal radials with sagittal and lateral keels.

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LARVAL DEVELOPMENT OF *EUPHAUSIA EXIMIA* (CRUSTACEA: EUPHAUSIACEA) WITH NOTES ON ITS VERTICAL DISTRIBUTION AND MORPHOLOGICAL DIVERGENCE BETWEEN POPULATIONS

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ABSTRACT

Larval development of *Euphausia eximia* includes the following stages: nauplius I-II, metanauplius, calyptopis I-III, and furcilia I-VI. The larvae are similar to those of congener *E. gibboides* but differ in both morphological detail and timing of developmental events.

A comparison of larvae of *E. eximia* from across the species' range showed significant differences in morphology between forms from the California Current terminus off Baja California and from the South Equatorial and Peru Currents. This variation may be evidence of genetic divergence between populations and perhaps indicates that the oxygen-deficient warm waters of the eastern tropical Pacific form an effective barrier between reproductive centers of the species. Significant differences in morphology were found as well during a preliminary survey of adults; the southern limit of the northern form of *E. eximia* was about latitude 2° north.

The vertical distribution of larval stages in day and night samples from two locations off Baja California and one in the South Equatorial Current showed development of diurnal vertical migration in the second half of the furcilia phase after acquisition of the full complement of setose abdominal pleopods. A "reverse" migration pattern was seen among calyptopes at two stations with the majority of larvae occurring in the surface stratum during the day and below the surface layer at night; larvae at the third station were found, both day and night, in the surface stratum until the onset of vertical migration. Variation in growth rate between areas within the range of each population may be correlated with relative abundance of food and duration of stay in food-rich surface waters.

Euphausia eximia Hansen is endemic to the eastern tropical Pacific, ranging from lat. 32°-34° N to 30° S and with areas of relative abundance in waters of the California Current terminus off Baja California and the Gulf of California, in the South Equatorial Current, and in the Peru Current (Brinton 1962; Antezana-Jeréz 1978). In a recent study of the horizontal and vertical distribution of euphausiids along a transect from ca. lat. 23° N, long. 115° W to lat. 3° S, long. 88° W, Brinton (1979) observed that *E. eximia* occurred sparsely between lat. 11° and 20° N but achieved high densities in the productive zones marginal to the oxygen-deficient portion of the eastern tropical Pacific. He noted that "Reproduction, as determined by presence of larvae, was not observed between 2° and 20° N; occurrences of juvenile and adult *E. eximia* in this zone, therefore, appear due to meridional advection from the northern (21° to 25° N) and equatorial population centers." This agreed with earlier observations of *E. eximia* in these areas (Brinton 1962).

Within the genus *Euphausia*, *E. eximia* is most closely related in adult morphology to *E. americana*, an Atlantic species, and to *E. krohnii*, found in both the Atlantic and Mediterranean (Mauchline and Fisher 1969). The larvae of *E. krohnii* have been described (Frost 1934; Casanova 1974) but those of *E. americana* have not yet been identified. The literature on larval development within the Euphausiacea has been reviewed by Gopalakrishnan (1973).

The purpose of this paper is to describe the larval development of *E. eximia* in the reproductive area of the California Current terminus population, to note the differences observed in morphology of larvae from the South Equatorial-Peru Current population and apparent variation within each population in rate of growth, and to provide information on the vertical distribution of larval stages.

METHODS

Larvae of *E. eximia* were sorted from preserved samples of plankton taken in the eastern Pacific (Figure 1) during Scripps Institution of Oceanog-

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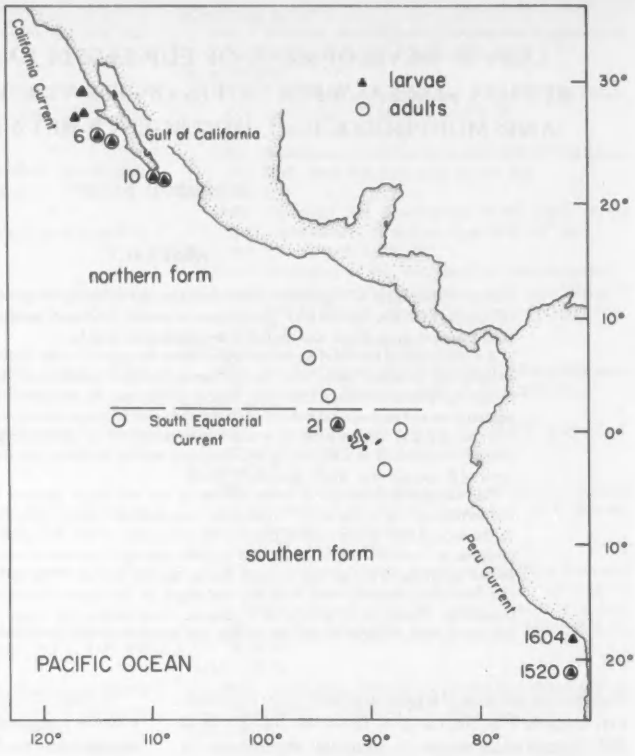

FIGURE 1.—Occurrence of northern and southern forms of *Euphausia eximia* in plankton samples from the eastern Pacific Ocean; Krill Expedition station numbers locate samples in which vertical distribution and growth of larvae were studied.

raphy Expeditions Krill, Aries, and Muddauber, and CalCOFI Cruise 5804. They were identified from an area off western Baja California in which *E. eximia* is consistently abundant and where closely related species (*E. mutica* and *E. recurva*), whose larvae we have identified, are rarely, if ever, present (Brinton 1967). At three locations (Stations 6, 10, and 21) larvae were counted as well in separate day and night series of tows taken across eight strata above 500 m on Krill Expedition (Brinton 1979) to investigate patterns of vertical distribution.

Larvae from each sample were grouped by size, information from length-frequency histograms, and degree of morphological differentiation into developmental stages which, to furcilia IV, were discrete and assumed to be separated by one molt. Furcilia V-VI and juvenile I were also presumed to be one intermolt although individual variation in growth and morphogenesis made boundaries less distinct. Altogether 2,210 individuals were measured and 347 dissected for study of appendages. Measurements were made with an ocular micrometer; the method was the same as that used in studies of species of the *E. gibboides* group (Knight 1975, 1978). In the comparison of growth rate between areas within each population larvae from Stations 1520 and 1604 were treated as one sample. Larvae were dissected in glycerine and at least 10 specimens of each stage were examined in detail. In the description of larval stages, the usual setation or condition noted is given in parentheses following the range observed. Drawings were prepared with the drawing attachment of a Wild M20 Microscope.[2]

The nomenclature used to describe larval morphology was modified from the studies cited above with respect to the mandible. It appears appropriate to refer to the dentate process near incisor

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

teeth of the right mandible as the lacinia mobilis (Weigmann-Haass 1977; Hessler[3]). In species of *Euphausia* I have examined in detail (*E. gibboides*, *E. sanzoi*, *E. fallax*, *E. pacifica*), in *Nematoscelis difficilis* (Gopalakrishnan 1973), and *Nyctiphanes couchii* (Le Roux 1976), the lacinia mobilis appeared only on the right mandible; it was found on the left mandible of *E. hanseni* by Weigmann-Haass (1977). Leg 1 is referred to as maxilliped through the furcilia phase.

Adults were sorted from a set of samples (Figure 1) for preliminary exploration of morphological differences between populations of *E. eximia*. The animals were sexed, measured to the nearest millimeter, and the armature of telson and inner process of segment 2 of antennular peduncle were inspected.

Gravid females of *E. eximia*, captured in nighttime plankton tows with a 1 m net from 200 m to the surface near Santa Catalina Island, were cultured aboard ship using the methods described by Lasker and Theilacker (1965). Larvae hatched from eggs spawned by one of the females were held through calyptopis I to confirm identification of early larval stages.

RESULTS

Observations of Reared Animals

Two gravid females spawned on the night of capture; they were 25.7 and 26.6 mm total length (TL) and shed 154 and 196 eggs. Their ovaries were blue before spawning and the embryos of the newly laid eggs were pale blue; the color faded before hatch. Of 154 eggs allowed to develop, 90% hatched and, at 17°-19° C room temperature, the duration of early larval stages was approximately as follows: 24 h for the egg; 24 h for nauplius I and II together; 48 h for the metanauplius. The first calyptopis appeared on the fourth day after spawn. These stages encounter similar temperatures in the surface waters off Baja California.

The spent female molted 6 days after spawning without shedding more eggs; a spermatophore was not found on the preserved female or her exuvia. Three other ovigerous females survived capture and molted twice, with 4 days between molts, without spawning; each shed a spermatophore with the exuvia during the first molt and the ovaries remained blue.

[3]Robert R. Hessler, Professor of Oceanography, Scripps Institution of Oceanography, Univ. Calif., La Jolla, CA 92037, pers. commun. July 1978.

Description of Larval Stages

Larval development in the California Current population (northern form) of *Euphausia eximia* included the following stages: nauplius I and II; metanauplius; calyptopis phase, three stages; furcilia phase, six stages. The stage which followed furcilia VI usually (in 92% of 53 individuals) had the adult number of spines on the telson (one terminal and two pairs posterolateral) and is referred to here as juvenile I. The observed furcilia stages are listed in Table 1 along with the development of pleopods, telson, and antenna. Measurements of the calyptopis, furcilia, and juvenile stages are given in Tables 2 and 3.

TABLE 1.—Development of pleopods, telson spines, and antenna in furcilia I-VI and juvenile I in the northern and southern forms of *Euphausia eximia*; ′ = pair nonsetose pleopods, ″ = pair setose pleopods.

Stage	Pleopod development	Telson spines		Form of antenna	Number of larvae	
		Terminal	Posterolateral		Northern form	Southern form
Furcilia I	1′	7	3	Natatory	151	72
Furcilia II	1″4′	7	3	Natatory	132	80
Furcilia III	5″	7	3	Natatory	334	104
		6	3		0	9
		5	3		1	4
		4	3		0	3
		3	3		1	5
Furcilia IV	5″	6	3	Juvenile	2	0
		5	3		8	0
		4	3		16	0
		3	3		128	2
		2	3		85	5
		1	3		192	57
Furcilia V	5″	1	3	Juvenile	195	45
		1	2		0	1
Furcilia VI	5″	1	3	Juvenile	40	42
		1	2		19	25
Juvenile I	5″	1	3	Juvenile	4	0
		1	2		49	47

TABLE 2.—Measurements (millimeters) of metanauplius and calyptopis I-III in the northern form of *Euphausia eximia*.

Stage	Total length	Carapace length	Carapace width	Telson width
Metanauplius, n = 123:				
Range	0.46-0.51	—	0.33-0.39	—
Mean	0.49		0.35	
SD	0.01		0.01	
Calyptopis I, n = 127:				
Range	0.97-1.09	0.59-0.67	0.36-0.44	0.158-0.186
Mean	1.03	0.62	0.40	0.170
SD	0.02	0.02	0.01	0.006
Calyptopis II, n = 140:				
Range	1.58-1.76	0.75-0.81	0.40-0.46	0.195-0.242
Mean	1.67	0.78	0.43	0.224
SD	0.04	0.02	0.02	0.008
Calyptopis III, n = 140:				
Range	2.20-2.55	0.89-0.99	0.50-0.61	0.242-0.279
Mean	2.36	0.94	0.56	0.260
SD	0.06	0.02	0.02	0.009

Although there is variation in timing of events with respect to stage, the form, setation, and development of appendages are very similar in larvae of congeners *E. gibboides* and *E. eximia*. The descriptions with figures of *E. gibboides* larvae (Knight 1975) may be consulted for morphology and development of appendages of *E. eximia* which are figured and discussed in detail here only when necessary to contribute information specific to *E. eximia*. The setations of maxillule, maxilla, and pleopods in larvae of *E. eximia* are given in Tables 4, 5, and 6.

TABLE 3.—Measurements (millimeters) of furcilia I-VI and juvenile I in the northern form of *Euphausia eximia*.

Stage	Total length	Carapace length	Telson width
Furcilia I, n = 151:			
Range	2.87-3.19	0.81-0.87	0.232-0.270
Mean	3.02	0.84	0.250
SD	0.07	0.02	0.009
Furcilia II, n = 132:			
Range	3.41-3.84	0.89-1.01	0.195-0.232
Mean	3.59	0.94	0.219
SD	0.09	0.02	0.009
Furcilia III, n = 103:			
Range	3.84-4.46	0.97-1.13	0.158-0.214
Mean	4.13	1.05	0.188
SD	0.12	0.03	0.010
Furcilia IV, n = 269:			
Range	4.08-4.97	1.07-1.25	0.149-0.195
Mean	4.60	1.16	0.167
SD	0.15	0.03	0.008
Furcilia V, n = 158:			
Range	4.52-5.66	1.13-1.39	0.121-0.177
Mean	5.13	1.26	0.153
SD	0.23	0.05	0.008
Furcilia VI, n = 58:			
Range	5.09-6.06	1.19-1.45	0.112-0.158
Mean	5.55	1.34	0.138
SD	0.23	0.06	0.009
Juvenile I, n = 53:			
Range	5.45-6.79	1.35-1.64	0.112-0.149
Mean	6.15	1.49	0.131
SD	0.32	0.07	0.007

EGGS.—Perivitelline space relatively small, 50 spawned eggs with the following measurements: Outer diameter, 0.38-0.46 mm; mean, 0.45 mm; SD, 0.02 mm. Perivitelline space, 0.03-0.07 mm; mean, 0.06 mm; SD, 0.01 mm. Eighty-five eggs from the plankton differed slightly: Outer diameter, 0.40-0.48 mm; mean, 0.45 mm; SD, 0.01 mm. Perivitelline space, 0.03-0.07 mm; mean, 0.05 mm; SD, 0.01 mm.

NAUPLIUS I AND II.—Body ovoid, as figured for *E. gibboides*, with one pair long posterior spines in nauplius I and a second short outer pair in nauplius II; both stages with 3 pairs of functional appendages—antennule, antenna, and mandible. Seven hatched nauplius I larvae with the following dimensions: Length, 0.38-0.41 mm; mean, 0.39 mm; SD, 0.02 mm. Width, 0.25-0.27 mm; mean, 0.26 mm; SD, 0.01 mm.

TABLE 4.—Development of maxillule in the northern form of *Euphausia eximia*; exopod with 4 setae and endopod with 2 medial and 3 terminal setae in all stages; () = usual condition.

Stage	Endopod		Basal endite setae		Coxal endite setae	Pseudexopod	
	Segments	Lateral seta	Medial	Proximal		Presence	Anterior seta
Calyptopis I	2	0	3	0	7	–	0
Calyptopis II-III	2	0	5	0	7	–	0
Furcilia I	2	0	6-7(7)	0	8	–	0
Furcilia II	2	0	7	0-1(1)	8	–	0
Furcilia III	2	0	9	1	8-9(8)	–	0
Furcilia IV	1-2	0-1(0)	8-10(9)	1	8-9(9)	–	0
Furcilia V	1	1	8-10(9-10)	1-2(1)	8-9(9)	–/+(+)	0
Furcilia VI	1	1	9-13(10)	1-2	9-10(9)	+	0
Juvenile I	1	1	10-12(10-11)	1-2(2)	9-11(10)	+	0-1

TABLE 5.—Setation of maxilla in the northern form of *Euphausia eximia*; medial lobe five with 3 setae in all stages; () = usual condition.

Stage	Exopod	Endopod	Medial lobes			
			1	2	3	4
Calyptopis I-III	1	3	8	4	4	4
Furcilia I	1	3	8	4	4-5 (5)	4
Furcilia II	1	3	8	4	4-5 (5)	4
Furcilia III	1	3	8	4	5-6 (5)	4-5 (4)
Furcilia IV	1	3	8	4-6 (4)	5-6 (6)	5
Furcilia V	1	3	8	4-6 (5-6)	6-7 (6)	5-6 (5)
Furcilia VI	1-3 (1-2)	3-4	8	5-6 (6)	6-7 (6)	5-6 (6)
Juvenile I	2-6 (2-5)	3-6 (4)	8-9 (8)	6	6-9 (7)	6-7 (6)

METANAUPLIUS (FIGURES 2A, 3A).—Rostral hood of carapace fringed with spines, 3 pairs on anterior margin relatively long, a fourth anterolateral pair sometimes somewhat longer than surrounding spines; usually 3 shorter spines between medial pair of long spines, tiny spines rarely interspersed; other small spines variable in number. Dorsal crest high, rounded, with 2 small spines (frequently broken or bent in preserved

TABLE 6.—Setation of pleopods in the northern form of *Euphausia eximia*; () = usual condition.

	Pleopod I		Pleopod 2		Pleopod 3		Pleopod 4		Pleopod 5	
Stage	Exopod	Endopod	Exopod	Endopod	Exopod	Endopod	Exopod	Endopod	Exopod	Endopod
Furcilia I	0	0	—	—	—	—	—	—	—	—
Furcilia II	6	1	0	0	0	0	0	0	0	0
Furcilia III	6-8(6)	2	6	1	6	1	6	1	6	1
Furcilia IV	7-8(8)	2-4(3-4)	8-9(8)	2-3(2)	8	2-3(2)	7-8(8)	2-3(2)	6-8(7-8)	2
Furcilia V	8-10(9)	4-6(4)	8-10(9)	4-5(4)	8-10(9)	3-5(4)	8-10(9)	4	7-9(8)	3-4(4)
Furcilia VI	9-11(10)	4-6(6)	9-11(10)	4-6(6)	9-11(10)	5-6	9-11(9-10)	4-6(5-6)	8-10(8-9)	4-5(4)
Juvenile I[1]	10-13(11)	5-7(6)	11-12(11)	6-7(6)	11-12(11)	6-7(6)	10-12(11)	6-7(6)	9-11(9)	4-6(5)

[1]In juvenile I, 11, 13, and 7% of pleopods 1, 2, and 3 with 1 seta proximal to appendix interna on endopod in 30 individuals.

specimens). Small pair of papillae on anterior margin of body beneath carapace; Fraser (1936) described papillae as frontal sensory organs.

Antennule and antenna functional, mandible reduced, buds of maxillule, maxilla, and maxilliped present.

Abdomen short, posterior margin with 5 pairs of spines; relatively long third pair articulated with telson, shorter spines fused. The long spine is plumose in *E. gibboides* but appears nearly smooth (with tiny serrations sometimes visible) in *E. eximia*.

CALYPTOPIS I (FIGURES 2B, 3B).—Rostral hood of carapace fringed with spines curving medially on anterior margin and posteriorly on posterolateral curve of hood; posterior margin of carapace produced into small dorsal spine; dorsal crest without spines. Striated body of photophore visible in developing compound eye, ocular papillae situated medially slightly below anterior margin of eye.

Mandibles (Figure 4a) with asymmetrical median armature and with anterolateral process but without lateral knob seen in species of the *E. gibboides* group (lateral knob is not found in any stage of *E. eximia*); anterolateral process, representing palp (Gurney 1942), decreases in size until furcilia V.

Maxillule and maxilla functional.

Maxilliped (Figure 5a) with form and setation as in *E. gibboides*: coxa with 4 setae on inner margin and 1 seta on posterior face; basis with 5 setae on inner margin and 1 distal submarginal seta, 1 marginal seta noticeably stout; endopod 2-segmented, proximal segment with 3 setae, 2 marginal and 1 submarginal, 1 marginal seta small and stout, distal segment with 4 terminal setae; exopod with 4 terminal setae and 1 lateral seta near articulation with basis. In *E. gibboides* the stout setae of endopod segment 1 and basis are nearly equal in length.

Abdomen unsegmented.

Telson (Figure 6a) with 1 pair lateral, 3 pairs posterolateral, and 6 terminal spines, middle posterolateral spine slightly longer than other spines.

CALYPTOPIS II (FIGURES 2C, 3C).—Carapace with lateral margins of rostral hood curved ventrally around body so that in dorsal view marginal spines are visible only on anterior margin of carapace.

Maxilliped with stout seta of endopod segment 1 and basis now about equal in length, as figured for calyptopis III (Figure 5b).

Abdomen with 5 segments.

Telson (Figure 6b) with 7 terminal spines, middle posterolateral spine relatively long, armature of telson spines as in *E. gibboides*.

CALPYTOPIS III (FIGURES 2D, 3D).—Carapace still with marginal spines of rostral hood visible in dorsal view only on anterior margin which extends well beyond eyes; lateral margins with denticle. Pigment sometimes visible in developing compound eyes; ocular papillae small, set farther out on eyestalk.

Maxilliped (Figure 5b) endopod with 5 setae on terminal segment unlike species of *E. gibboides* group which retain 4 setae in this stage, coxa with 6 setae.

Abdomen with 6 segments, sixth segment with pair of biramous uropods.

FURCILIA I (FIGURES 7A, 8A).—Carapace with rectangular rostral plate fringed with marginal spines which curve toward small median spine or denticle; posterior margin with dorsal spine. Eyes movable, pigmented, with rounded contour in furcilia stages (Figure 8d) unlike lobed contour of *E. gibboides* eye.

Bud of leg 2 present.

Abdomen with one pair nonsetose pleopods on segment 1.

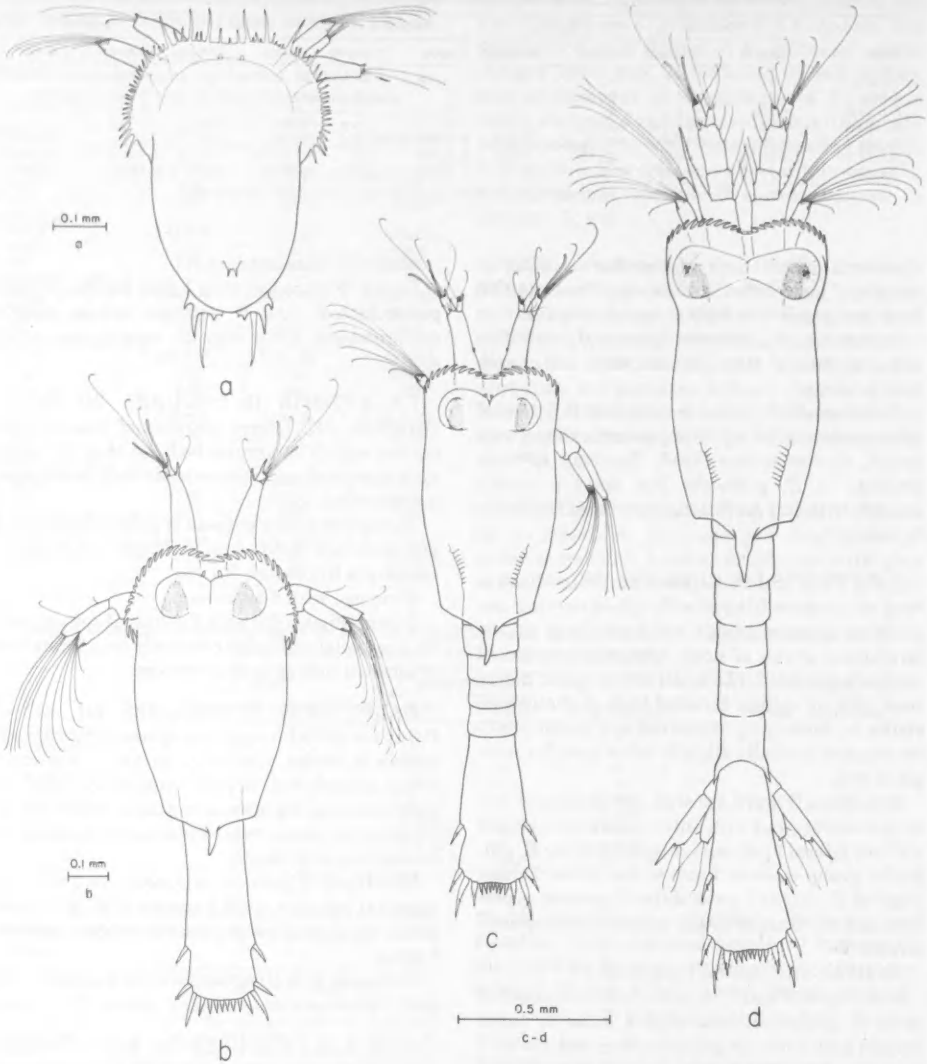

FIGURE 2.—*Euphausia eximia*, northern form, dorsal view: a, metanauplius; b-d, calyptopis I-III.

FURCILIA II (FIGURES 7B, 8B).—Carapace with narrower rostral plate and larger median spine, posterior margin without dorsal spine.

Maxilliped endopod with 5 or 6 (5) setae on distal segment.

Leg 2 endopod with 3-5 (4) segments, 1 or 2 (2) terminal setae, and variable marginal setation; exopod nonsetose; gill with two lobes; developing photophore may be visible.

Leg 3 unsegmented, nonsetose, with bud of exopod and bifid gill bud.

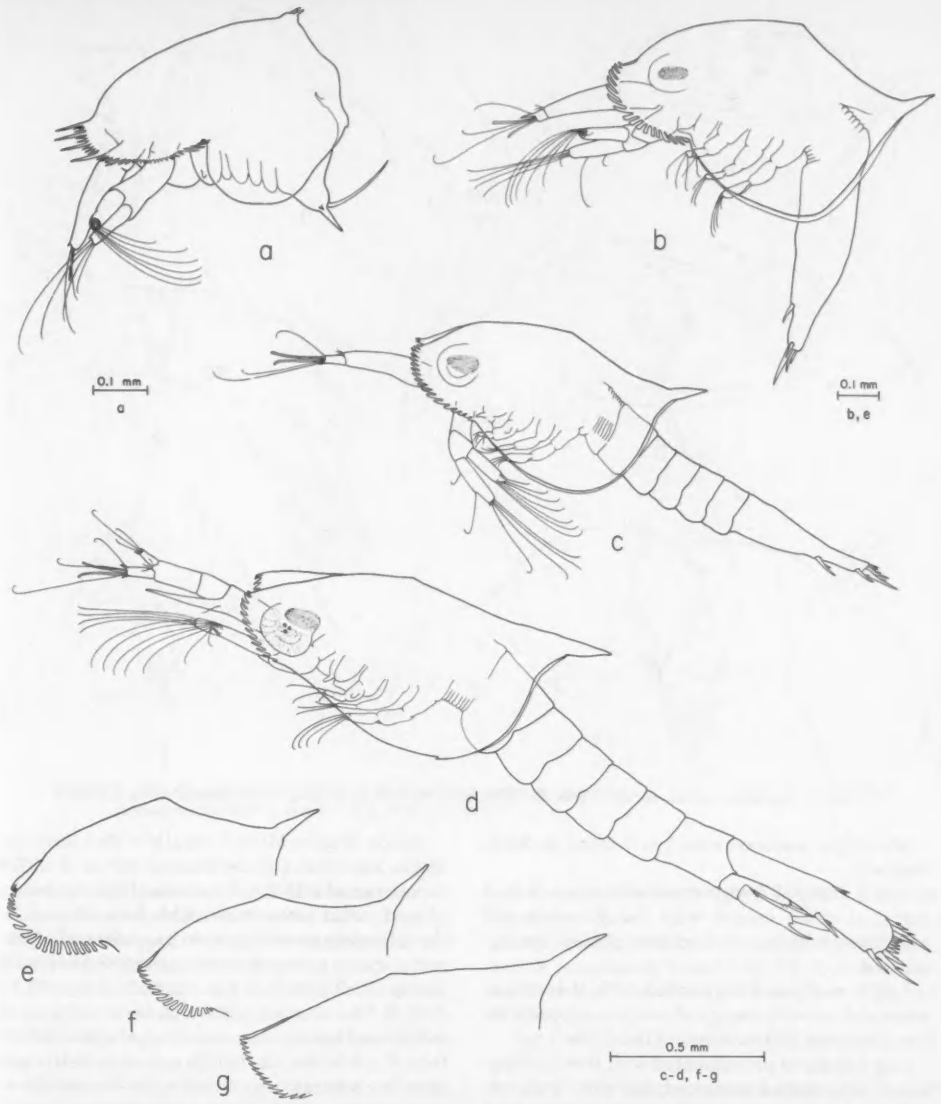

FIGURE 3.—*Euphausia eximia*, lateral view. Northern form: a, metanauplius; b-d, calyptopis I-III. Southern form: e-g, calyptopis I-III.

Buds of legs 4 and 7 sometimes present.

Abdomen with one pair setose pleopods on segment 1 and 4 pairs nonsetose pleopods on segments 2-5; photophore on segment 1 pigmented, photophore of segment 4 sometimes forming.

FURCILIA III (FIGURES 7C, 8C).—Carapace with rostrum narrower and lengthening.

Antennule with flagella lengthening, often 2-segmented; 1 of 2 aesthetes on outer ramus bifurcate distally as in *E. gibboides* furcilia III.

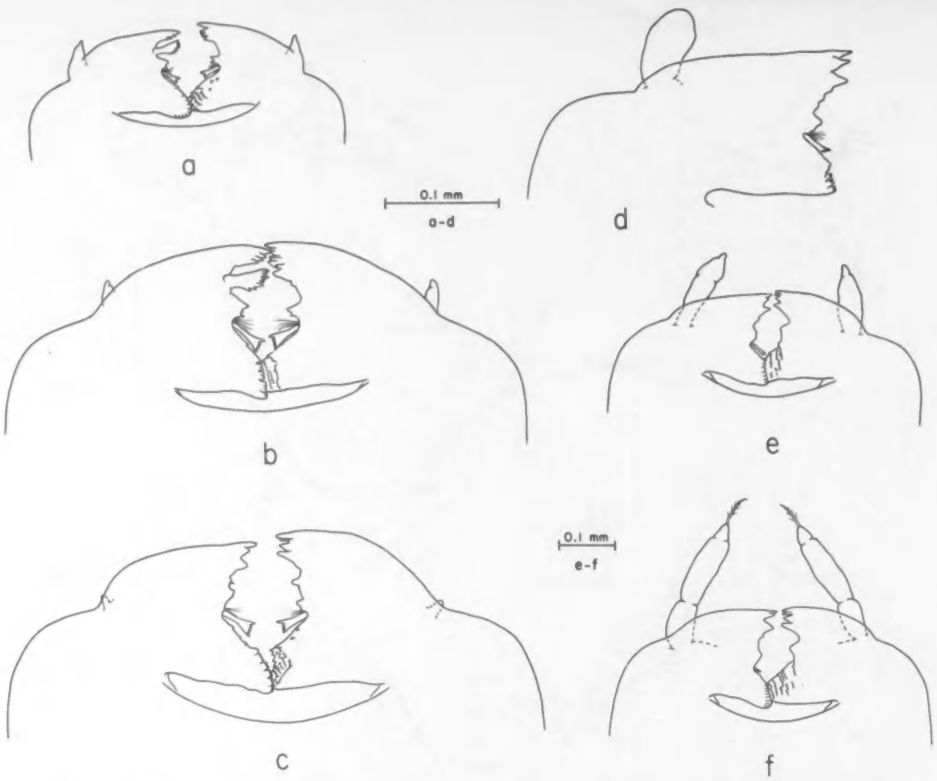

FIGURE 4.—*Euphausia eximia*, northern form. Mandible, posterior view: a, calyptopis I; b-e, furcilia III-VI; f, juvenile I.

Maxilliped endopod with 5 or 6 setae on distal segment.

Leg 2 endopod 5-segmented with more than 2 terminal setae; exopod with 2-4 (3) setae; gill sometimes with bud of third lobe; photophore pigmented.

Leg 3 endopod 5-segmented with 2 terminal setae and variable marginal setation; exopod with 0 or 1 (0) seta; gill with bud of third lobe.

Leg 4 endopod unsegmented with 0 or 1 (0) terminal seta; exopod nonsetose; gill with two lobes.

Leg 5 rudimentary, sometimes with buds of exopod and gill.

Leg 7 with bifid gill and developing photophore visible.

Bud of leg 8 sometimes present.

Abdomen with 5 pairs setose pleopods; photophores pigmented on segments 1 and 4 and forming on segment 2.

Telson (Figure 6f) still usually with 7 terminal spines and 3 pairs posterolateral spines (2 of 336 larvae varied with 3 and 5 terminal spines); telson of next instar sometimes visible beneath cuticle, the following percentages (in parentheses) of terminal spines were observed among 293 furcilia III larvae: 7(1.0), 6(0.3), 5(1.4), 4(2.4), 3(30.4), 2(15.7), 1(48.8). The setation pattern on inner margins of middle and innermost posterolateral spines differs from *E. gibboides*; the middle spine has 3 stronger spinules separated by small spinules and inner spine bears several spinules distally.

FURCILIA IV (FIGURES 7D, 9A).—Carapace with a few small spines on lateral margins of rostrum and stronger median spine.

Antennular flagella with 8 or 9 segments, one of the paired aesthetes on outer ramus no longer bifurcate.

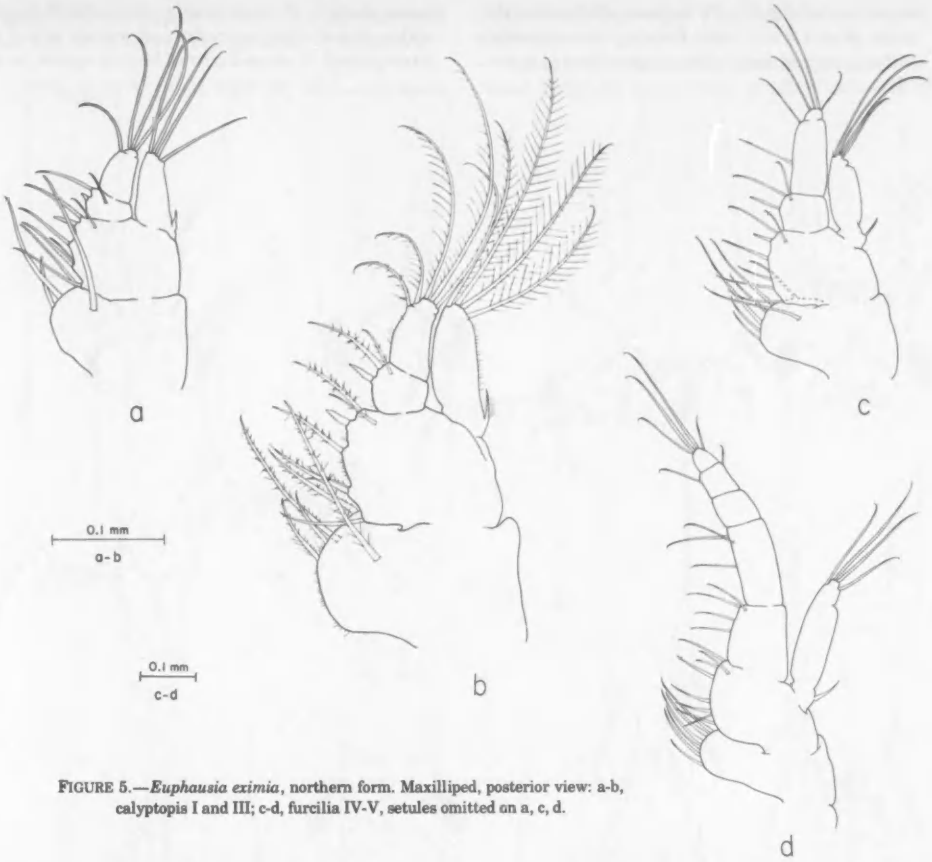

FIGURE 5.—*Euphausia eximia*, northern form. Maxilliped, posterior view: a-b, calyptopis I and III; c-d, furcilia IV-V, setules omitted on a, c, d.

Antenna (Figure 10a) modified from natatory to juvenile form, scale (exopod) with 11-13 (12) setae, flagellum (endopod) with 4-6 (4) segments, 2 or 3 (2) peduncular and 2-4 (2) flagellar.

Mandible (Figure 4c) modified with fewer, somewhat broader incisor teeth and lacinia mobilis missing or very much reduced; anterolateral process very small.

Maxilliped (Figure 5c) with 5 or 6 (6) setae on distal segments of lengthening endopod; basis and coxa with 6-8 (6-7) setae.

Leg 2 exopod with 5 or 6 (5) setae, gill with three lobes.

Leg 3 endopod with >2 terminal setae, exopod with 4-6 (5) setae; gill with three lobes, rarely with bud of fourth lobe.

Leg 4 endopod 5-segmented with 2-5 (2) terminal setae, exopod with 0-4 (0-2) setae; gill with small third lobe.

Leg 5 endopod usually unsegmented (ca. 3 segments occasionally seen) with 0-2 (0-1) terminal setae; exopod nonsetose; gill sometimes with bud of third lobe.

Leg 6 rudimentary with exopod bud and 2 or 3 gill buds.

Leg 7 with lightly pigmented photophore and three-lobed gill; leg 8 with three gill lobes.

Abdomen with photophores pigmented on segments 1, 2, and 4, and sometimes forming on segment 3.

Telson (Figure 6g) with 6-1 terminal spines and 3 pairs posterolateral spines (Table 1), 45% of 431 furcilia IV with 1 and 30% with 3 terminal spines (frequencies similar to those observed on develop-

ing telson of furcilia IV in premolt furcilia III); telson of next instar when forming beneath cuticle with 1 terminal and 3 pairs posterolateral spines. Inner margin of innermost posterolateral spine with series of strong spinules and shorter spinules interspersed. A second pair of lateral spines, or a

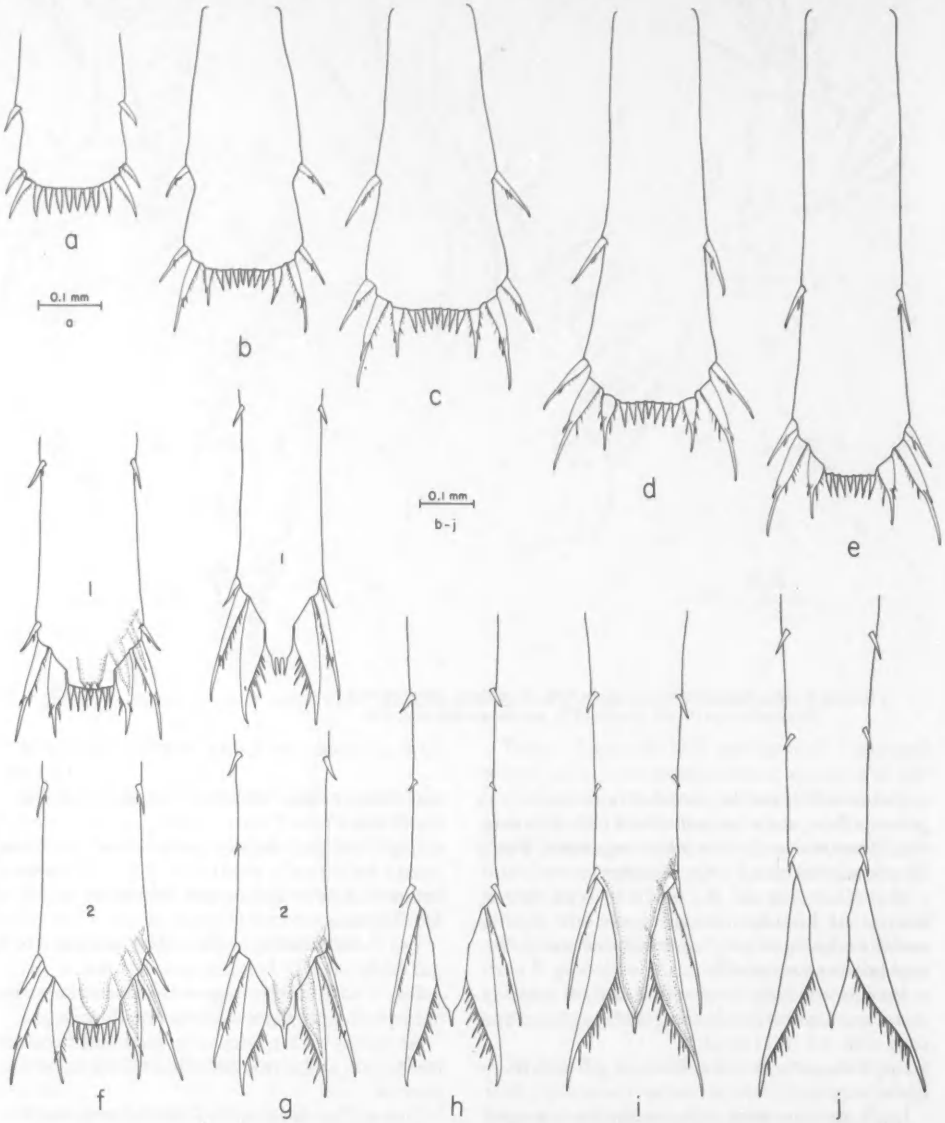

FIGURE 6.—*Euphausia eximia*, northern form. Telson, dorsal view: a-c, calyptopis I-III; d-e, furcilia I-II; f, furcilia III, 1-premolt to 3 terminal spines, 2-premolt to 1 terminal spine; g, furcilia IV, 1-with 3 terminal spines, 2-with 1 terminal spine; h-i, furcilia V-VI; j, juvenile I.

single additional spine on one side only, was found on 48% of 87 larvae examined for this feature.

FURCILIA V (FIGURES 7E, 9B).—Carapace with or without a few tiny lateral denticles on rostrum.

Antennule with lateral spine of peduncle segment 1 slightly longer than or equal to length of

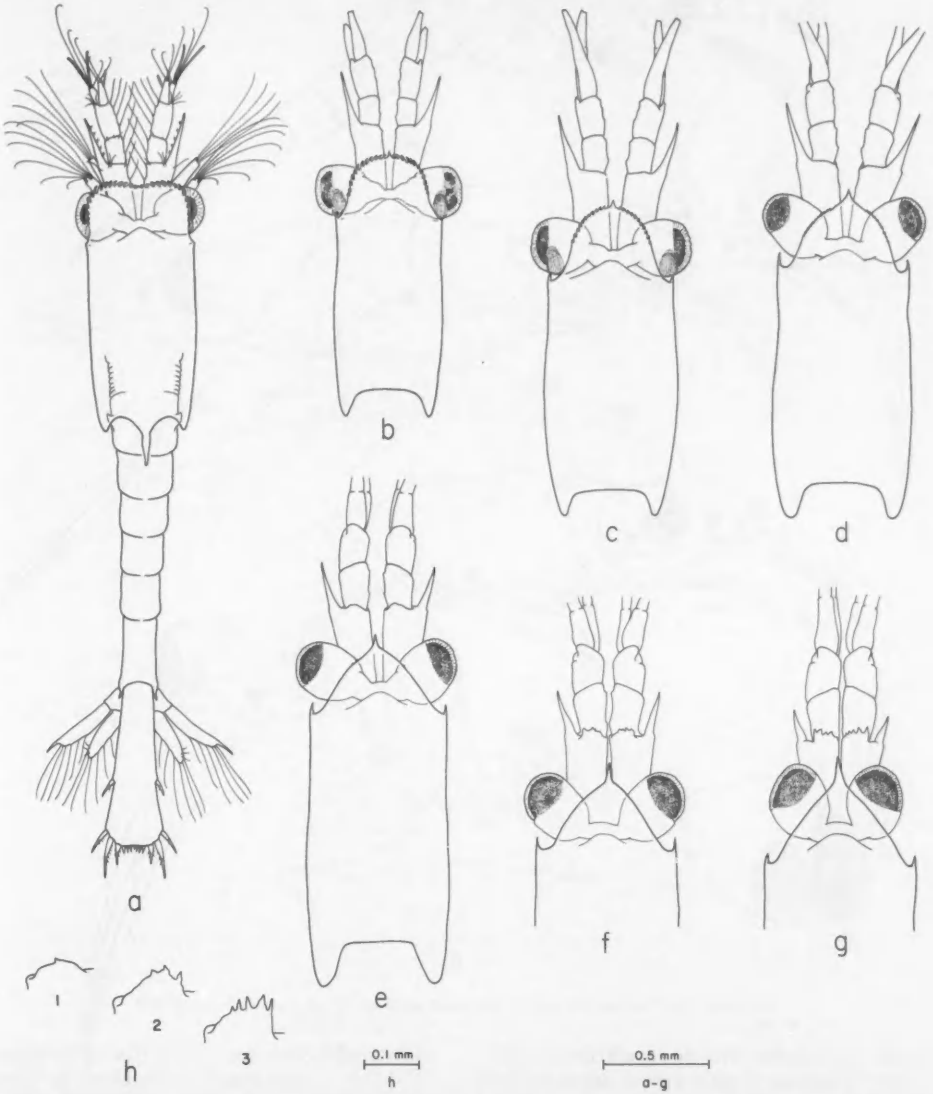

FIGURE 7.—*Euphausia eximia*, northern form, dorsal view: a-f, furcilia I-VI; g, juvenile I; h1-3, typical development of dorsal lappet on segment 1 of antennular peduncle in furcilia V-VI and juvenile I

segment 2, sometimes small variable rudiment of dorsal lappet present on segment 1 of peduncle with margin smooth or extended into 1 or 2 small knobs (Figure 7h-1); no specimens with flagella intact.

Antennal scale with 13-16 (14-15) setae and

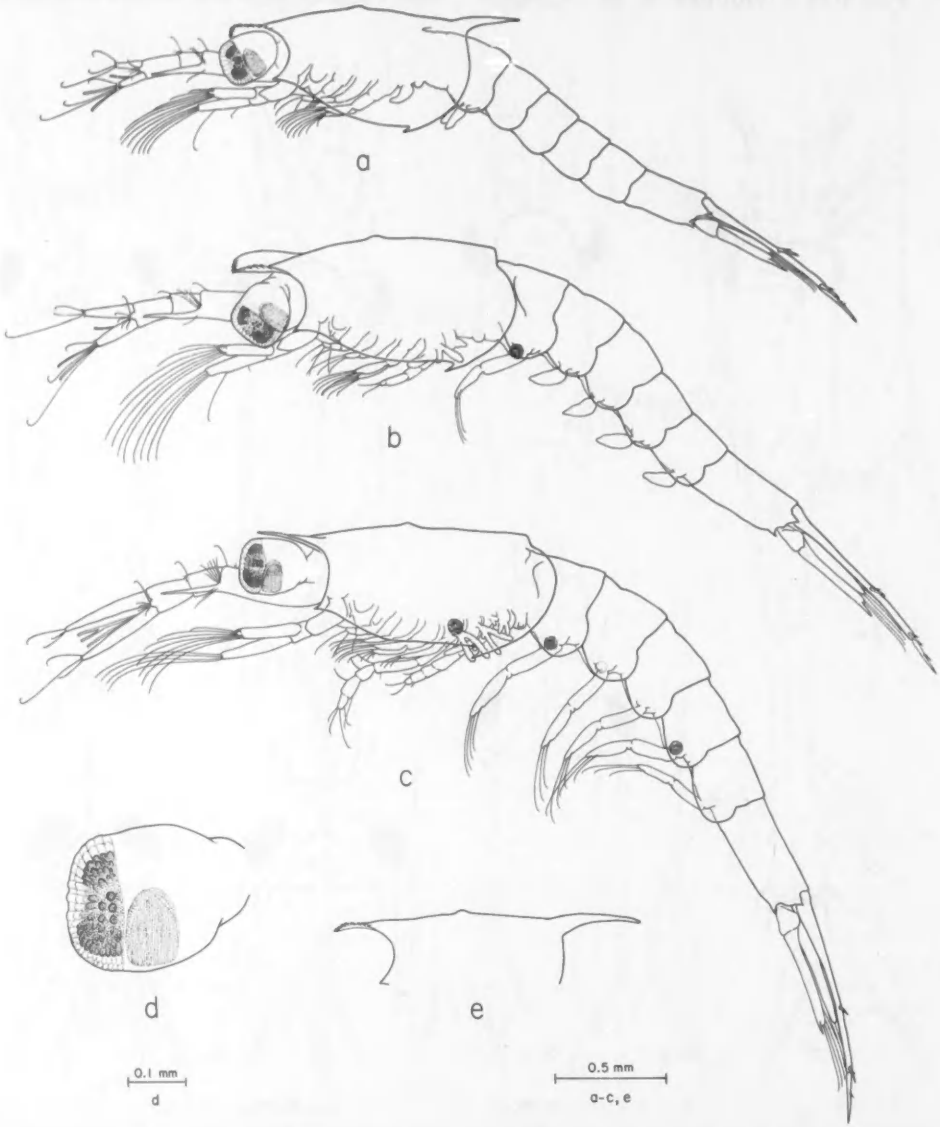

FIGURE 8.—*Euphausia eximia*, lateral view. Northern form: a-c, furcilia I-III; d, eye of furcilia II. Southern form: e, carapace of furcilia I.

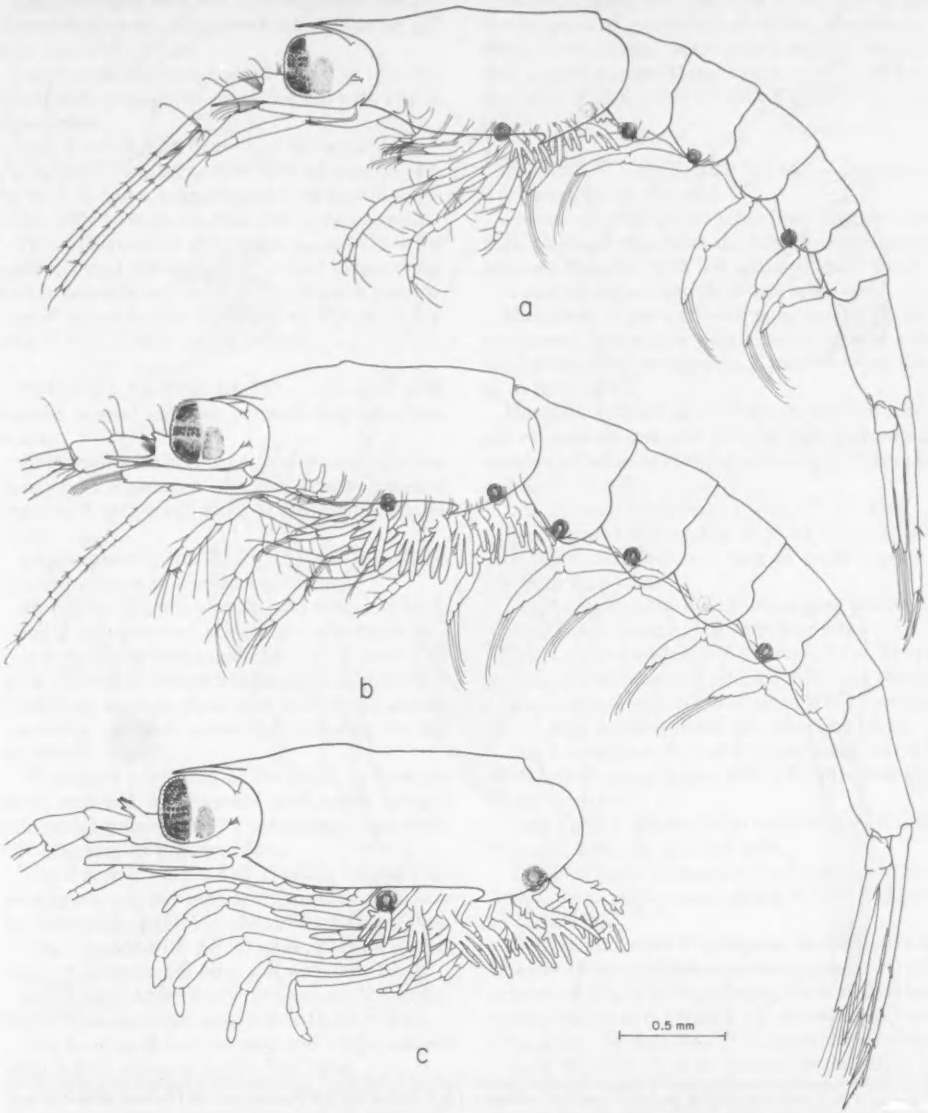

FIGURE 9.—*Euphausia eximia*, northern form, lateral view: a-b, furcilia IV-V; c, juvenile I.

flagellum usually with 12 segments, 3 peduncular and 7-10 (9) flagellar (Figure 10b).

Mandible (Figure 4d) without remnant of lacinia mobilis, palp lengthening.

Maxilliped (Figure 5d) with endopod now about equal in length to knee of leg 2, basis with 7-9 (8), and coxa with 6-8 (6) setae and usually without long seta on posterior face.

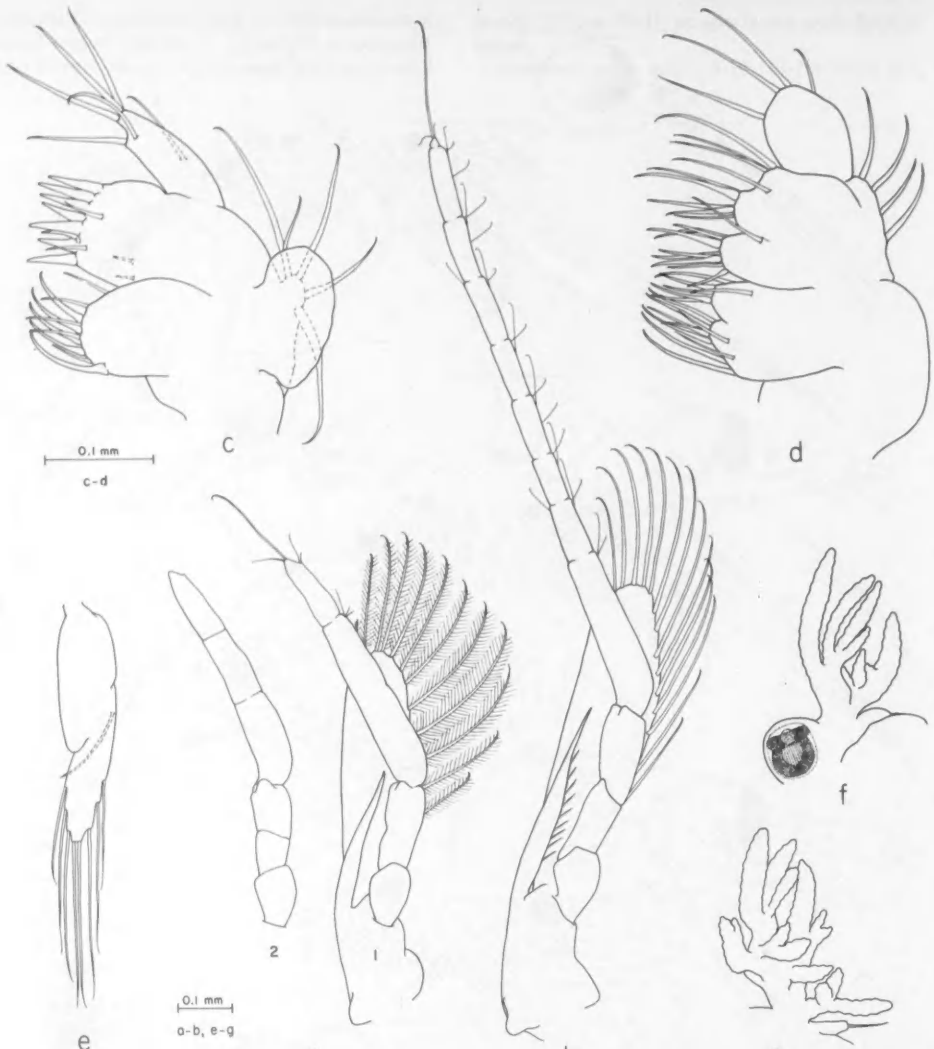

FIGURE 10.—*Euphausia eximia*, northern form. Antenna, ventral view: a 1-2, furcilia IV with variation in segmentation of endopod; b, furcilia V. Maxillule and maxilla, posterior view: c-d, juvenile I. Leg 2 exopod and legs 7-8: e-g, juvenile I (setules omitted in b-e).

Leg 2 exopod with 6 or 7 (6) setae, 1 of 28 appendages examined with additional proximal seta on inner margin common in furcilia VI and juvenile I (Figure 10e); gill sometimes with bud of fourth lobe.

Leg 3 exopod with 5-7 (6) setae, 1 of 34 appendages examined with proximal seta as on leg 2 exopod; gill sometimes with bud of fourth lobe.

Leg 4 endopod setose; exopod with 4-6 (5) setae; gill sometimes with bud of fourth lobe.

Leg 5 endopod with 4 or 5 (5) segments and 1-5 (2) terminal setae; exopod with 0-5 (0-2) setae; gill with bud of third lobe.

Leg 6 endopod unsegmented with 0 or 1 (0) terminal seta; exopod nonsetose and gill with two or three lobes.

Legs 7 and 8 with more than three gill lobes.

Abdomen with pigmented photophores on segments 1, 2, and 4, photophore on segment 3 sometimes with visible structure and some pigment.

Telson (Figure 6h) with 1 terminal and 3 pairs of posterolateral spines; telson of next instar when visible beneath cuticle with only 2 pairs posterolateral spines in 38% of 77 larvae; 97% of 71 furcilia V with 2 pairs lateral spines.

FURCILIA VI (FIGURE 7F).—Carapace with smooth lateral margins on well-developed rostrum.

Antennule with lateral spine about equal or less than length of peduncle segment 2, dorsal lappet of segment 1 with small knob or few spines (Figure 7h-2).

Antennal scale with 15-18 (16) setae; flagella no longer intact in preserved specimens.

Mandibles (Figure 4e) with palp relatively long, usually unsegmented, sometimes constricted into 2 or 3 weakly defined segments; 1 of 18 furcilia VI with 1 terminal seta on 2-segmented palp; slender terminally dentate plate near molar area of each mandible reduced, sometimes missing on left mandible.

Maxilliped continues to lengthen to juvenile form, endopod 5-segmented and setose, exopod still with 1 proximal and 4 distal setae, coxa without long seta on posterior face.

Leg 2 exopod with 6-8 (6-7) setae, 14 of 17 appendages examined with additional proximal seta on inner margin (Figure 10e); gill with four lobes.

Leg 3 exopod with 6-8 (6) setae, 22 of 24 appendages with proximal seta; gill with four lobes.

Leg 4 exopod with 6 or 7 (6) setae, 4 of 21 appendages with proximal seta; gill with four lobes.

Leg 5 endopod 5-segmented and setose; exopod with 4-6 (5) setae; gill with four lobes.

Leg 6 endopod with 0-5 (0-3) segments and 0-2 (1) terminal setae; exopod with 0-3 (0) setae; gill with four or more lobes.

Legs 7 and 8 with branching gill lobes, rudiment of leg 7 sometimes with terminal seta (Figure 10f).

Abdomen with photophores pigmented on segments 1-4.

Telson (Figure 6i) with 3 or 2 (in 32% of 59 larvae) pairs of posterolateral spines, developing telson of next instar when visible beneath cuticle with 2 pairs posterolateral spines in 18 of 19 larvae; 94% of 52 furcilia VI with 2 pairs of lateral spines.

JUVENILE I (FIGURES 7G, 9C).—Carapace with lengthening rostrum.

Antennule with lateral spine from slightly less than to about one-third the length of peduncle segment 2, lappet with 3-6 spines (Figure 7h-3).

Antennal scale with 16-19 (18) setae.

Mandibles (Figure 4f) with palp usually three-segmented, sometimes with 1 terminal seta and 0-3 lateral setae on segment 2, median armature as in furcilia VI.

Maxillule without or with seta on anterior margin of pseudexopod and maxilla with increasing numbers of setae on endopod and exopod (Tables 4, 5; Figure 10 c-d).

Leg 1 (maxilliped) exopod with 4-7 (4) setae.

Leg 2 exopod (Figure 10e) with 6-8 (8) setae, all with additional proximal seta on inner margin; gill with four lobes.

Leg 3 exopod with 6-8 (8) setae plus proximal seta on inner margin; gill with four lobes.

Leg 4 exopod with 6-8 (6-7) setae, 12 of 20 appendages with proximal seta; gill with four lobes.

Leg 5 exopod with 5-8 (6-7) setae, 3 of 17 appendages with proximal seta; gill with four lobes.

Leg 6 endopod with 4 or 5 (5) segments and 2-4 (2) terminal setae; exopod with 2-6 (2-3) setae; gill many branched.

Legs 7 and 8 (Figure 10f-g) rudiments each with terminal seta and ramified gills.

Telson (Figure 6j) usually with 2 pairs posterolateral and 2 pairs lateral spines (in 92% and 98% of 53 larvae).

In *E. eximia*, as in *E. gibboides*, the reduction in number of terminal telson spines appears not to be a reliable single guide to recognition of developmental stages in furcilia IV-VI but rather only one of a group of features that characterize these stages. Furcilia IV of *E. eximia*, as delimited in this study, had a variable number of terminal spines which overlapped with the number of terminal telson spines in furcilia III and V. Furcilia IV differed from furcilia III, however, in the following features: modification of both antenna and mandible; segmentation of antennular flagellum; setation of exopods of legs 2 and 3; setation and segmentation of leg 4 endopod; and setation of

pleopods 2-5. Furcilia IV was separated from furcilia V by the segmentation of antennal flagella, maxilliped endopod, and leg 5 endopod; and endopod setation of pleopods 2-5, with small overlap on pleopod 3 only. Grouping of stages by terminal telson spine number would not be supported by these characters and if, for instance, all larvae with 1 terminal and 3 pairs posterolateral telson spines were grouped together, the range in size within the stage would become uncomfortably large, more than twice that of furcilia III and almost twice that in furcilia V. Variability in reduction of posterolateral spines was seen in furcilia VI and rarely in juvenile I.

The number of telson spines did relate to variation in size within a stage. For instance, furcilia III larvae that would molt from 7 to 3 terminal spines were 0.04 mm smaller on the average than those that would molt from 7 to 1 terminal spine and in furcilia IV, larvae with 3 terminal spines were 0.08 mm smaller on the average than those with 1 terminal spine. Variation in morphology within a stage was assessed in a sample of larvae from one location, as by midfurcilia phase there was a noticeable difference in rate of development between areas within the range of the population. It may be seen, for example, in a comparison of the length of larval stages at two locations in the California Current terminus (Figure 11) that, although they were smaller on the average, furcilia VI larvae from Station 10 in the mouth of the Gulf of California were within the size range of juvenile I of the slower growing larvae from Station 6 off western Baja California. The patterns of telson spine reduction in furcilia III-VI and juvenile I at these two locations, shown in Table 7, exemplify variation within the stages which appears to reflect the difference in rate of growth and morphogenesis.

South Pacific Population

Larvae from two areas within the southern range of *E. eximia* (Figure 1) were compared with larvae from the California Current terminus and, although the populations were generally similar, discrepancies were discovered. The most conspicuous differences proved to be in the armature of the telson. Among larvae in the South Equatorial and Peru Current population (southern form), the middle posterolateral spine was longer relative to the other two posterolateral spines and the majority of larvae had one pair of lateral spines only in all stages (Figure 12, Table 8); northern form larvae had 2 pairs of lateral telson spines from furcilia V. Furcilia III was slightly more variable in number of terminal telson spines while furcilia IV was less variable (Table 1). The carapace differed also with relatively longer posterodorsal spines from calyptopis I to furcilia I (Figures 3e-g, 8e) and sometimes with slightly larger and more persistant marginal spines.

Development of appendages was usually similar in the two forms. The lateral spine of the antennule was sometimes shorter and the lappet less developed in southern form furcilia VI and the setation of maxillule basal endite differed: 20, 62, and 75% of larvae examined had acquired 2 setae on the proximal margin of endite in furcilia V, VI, and juvenile I among northern form larvae while only 0, 2, and 17% of southern form larvae had a second seta in these stages.

Southern form larvae were smaller on the average in the furcilia phase but, as in the California Current terminus, differences in growth per stage between areas within the range of the population were noted. Developmental stages of *E. eximia* from the Peru Current (Stations 1520/1604) were larger on the average than those from the South

TABLE 7.—Pattern of telson spine reduction in furcilia III-VI and juvenile I in the northern form of *Euphausia eximia* at two locations (Stations 6 and 10) in the California Current terminus. Values indicate percentage with telson armature in stage.

		Terminal + posterolateral telson spines							
Stage	Stn	7+3	6+3	5+3	4+3	3+3	2+3	1+3	1+2	*n*
Furcilia III	6	100.0	—	—	—	—	—	—	—	280
	10	97.0	—	1.5	—	1.5	—	—	—	68
Furcilia IV	6	—	0.7	2.9	5.1	36.7	21.1	33.5	—	275
	10	—	—	—	—	15.1	19.0	65.9	—	126
Furcilia V	6	—	—	—	—	—	—	100.0	—	41
	10	—	—	—	—	—	—	100.0	—	97
Furcilia VI	6	—	—	—	—	—	—	92.9	7.1	14
	10	—	—	—	—	—	—	21.4	78.6	14
Juvenile I	6	—	—	—	—	—	—	25.0	75.0	12
	10	—	—	—	—	—	—	—	100.0	24

TABLE 8.—Number of pairs of lateral telson spines in furcilia IV-VI, juvenile I, and adult in northern and southern forms of *Euphausia eximia*. Values indicate percentage with telson armature in stage.

		Pairs of lateral telson spines				
Stage	Form	1	2	3	4	*n*
Furcilia IV	Northern	51.7	48.3	—	—	87
	Southern	98.4	1.6	—	—	61
Furcilia V	Northern	2.8	97.2	—	—	71
	Southern	97.9	2.1	—	—	48
Furcilia VI	Northern	5.8	94.2	—	—	52
	Southern	100.0	—	—	—	67
Juvenile I	Northern	1.8	98.2	—	—	55
	Southern	95.0	5.0	—	—	60
Adult	Northern	5.6	85.7	7.9	0.8	126
	Southern	97.5	2.5	—	—	121

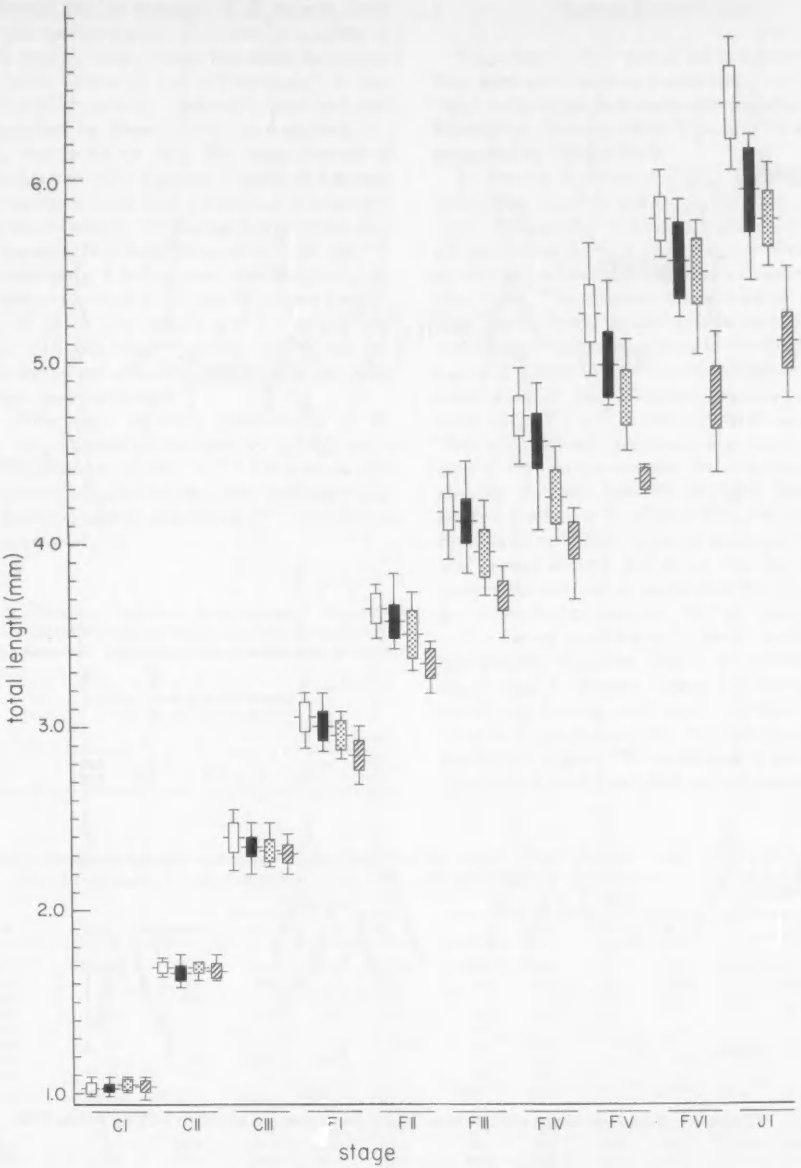

FIGURE 11.—Length of developmental stages of northern and southern forms of *Euphausia eximia* at four locations: mouth of Gulf of California, Station 10 (white); west of Baja California, Station 6 (black); Peru Current, Stations 1520/1604 (dots); South Equatorial Current, Station 21 (diagonal lines); vertical lines indicate range, horizontal lines indicate mean, and rectangles indicate sample standard deviations.

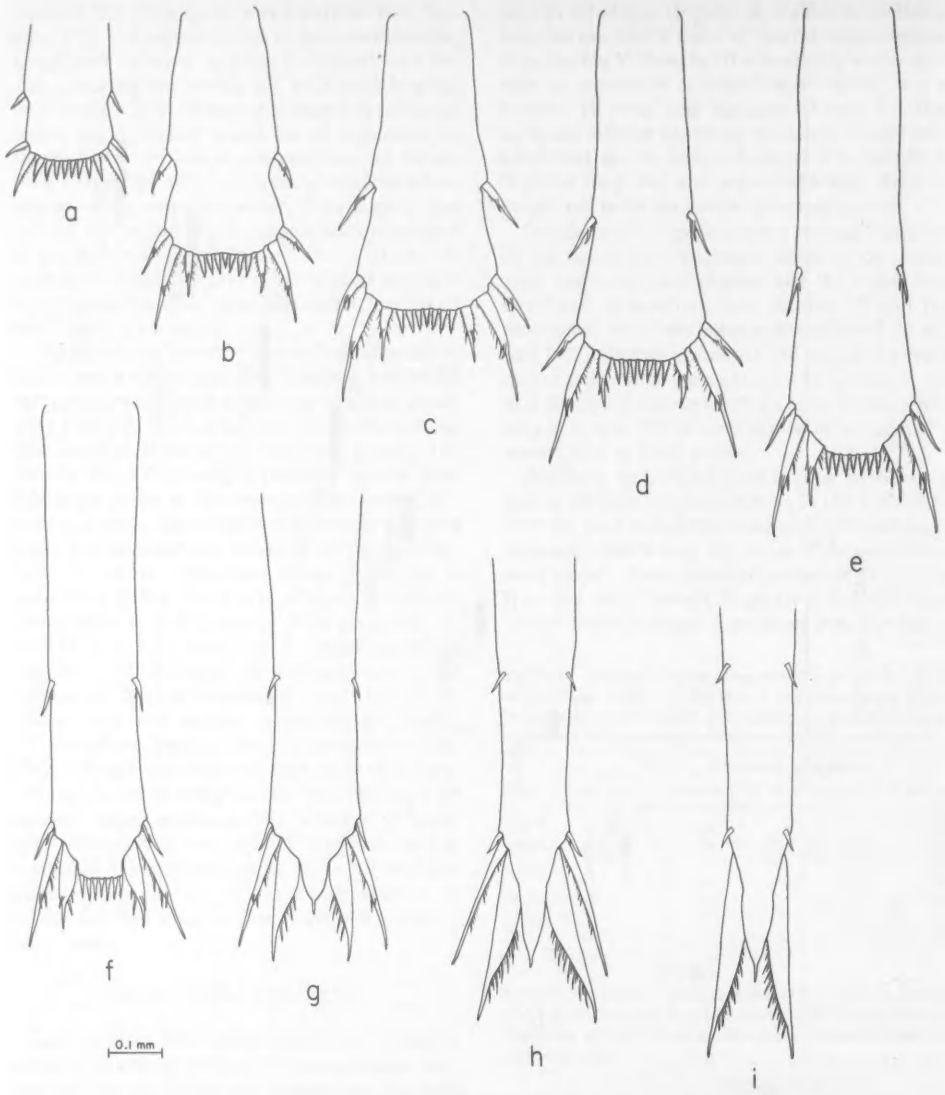

FIGURE 12.—*Euphausia eximia*, southern form. Telson, dorsal view: a-c, calyptopis I-III; d-i, furcilia I-VI.

Equatorial Current (Station 21). The lengths of larvae from these two locations are compared in Figure 11 (there were few furcilia V at Station 21 and consequently a small range in total length of this stage). Proportions of carapace length and telson width to total length were, on the average, as in northern form larval stages.

Because of the differences encountered between northern and southern form larvae, a preliminary survey of a few adult morphological characters

was carried out on samples of *E. eximia* from across the species' range. Variation in number of pairs of lateral telson spines was found to persist in the adult (Table 8) and a discrepancy in the armature of antennular peduncle, described and photographed by Roger (1967) in equatorial *E. eximia*, was found as well. The inner process of antennular peduncle segment 2 had 1 or 2 spines in the northern form and 1-5 spines in southern form adults (Table 9) and the number of spines was related to size. Northern form adults <21 mm TL had 1 spine only; 1 or 2 spines were found only on the largest animals of 21-27 mm. Southern form *E. eximia* of 12-18 mm length had 1-4 spines but animals >18 mm had 2-5 spines; 1 spine was not seen on the larger adults. Armature of the process was often asymmetrical.

The differences between populations of *E. eximia* in frequency of numbers of lateral spine pairs on the telson of furcilia V-VI and adult, and in armature of adult antennular peduncle segment 2 proved highly significant ($P = <0.005$) in chi-square analyses.

TABLE 9.—Number of spines on inner process of antennular peduncle segment 2 in adults of the northern and southern forms of *Euphausia eximia*. Values indicate percentage with armature in form.

	Number of spines on inner process, antennular peduncle segment 2					
Form	1	2	3	4	5	Number
Northern	93.2	6.8	—	—	—	117
Southern	21.2	33.9	33.1	11.0	0.8	118

Vertical Distribution

When larvae were sorted for taxonomic study, they were also counted at three stations in day and night series of vertical samples taken during Krill Expedition (Brinton 1979). The data obtained are presented in Tables 10-12.

At Station 6, west of Baja California in the California Current (Table 10), the distribution of eggs corresponded with the nighttime range of adults indicating that the majority of female *E. eximia* had spawned in the surface waters during the night. The highest concentration of metanauplii was found in the layer below the surface, reflecting sinking of eggs prior to hatching (Mauchline and Fisher (1969) note that eggs of *Thysanoessa raschii* and *Meganyctiphanes norvegica* sank at 5.5-7.5 m/h in water of 33.3‰ and 15° C). The majority of calyptopes and early furcilia stages were in the surface layer during the day, sinking to strata beneath at night. The pattern shifted gradually in midfurcilia phase and from furcilia III, the stage when all pleopods are setose, the larvae moved deeper in the daytime and toward the surface at night, and developed stronger migrating capability with increasing size.

The larval population structure and distribution pattern varied at Station 10 in the mouth of the Gulf of California (Table 11). No eggs were found and larvae were most abundant in early furcilia stages instead of in the metanauplius and calyptopis phases. The metanauplii were seen at the surface, and there was no evidence of nightly

TABLE 10.—Vertical distribution (percentage of stage at depth) of larvae and adults of *Euphausia eximia* in day and night samples from the California Current terminus off western Baja California (Station 6) and number/1,000 m³ in each stage.

			Calyptopis			Furcilia						
Depth (m)	Eggs	Metanauplius	I	II	III	I	II	III	IV	V	VI	Adult
Day:												
0-43	97.2	26.2	99.6	99.5	100.0	99.3	95.0	67.7	51.4	40.5	—	—
43-86	2.4	73.6	0.3	—	—	—	5.0	16.5	18.0	33.1	60.0	—
86-129	—	0.1	—	—	—	—	—	12.8	14.9	13.5	—	—
129-172	—	—	—	—	—	—	—	3.0	15.7	10.8	40.0	—
182-275	0.3	(<0.1)	0.1	0.1	—	—	—	—	—	—	—	100.0
275-368	0.1	0.2	—	—	—	—	—	—	—	—	—	—
368-461	—	—	(<0.1)	0.1	—	0.7	—	—	—	—	—	—
461-554	—	—	—	—	—	—	—	—	—	—	—	—
No./1,000 m³	3,283	10,593	7,510	3,835	991	288	100	436	255	37	5	28
Night:												
0-43	88.1	5.7	1.3	1.5	3.8	0.7	0.8	11.1	48.8	50.0	77.8	69.1
43-86	8.4	79.5	70.7	54.5	41.1	52.9	70.7	74.4	51.2	50.0	22.2	15.6
86-129	3.5	14.8	28.0	44.0	55.0	46.4	28.4	14.5	—	—	—	15.3
129-172	—	—	—	—	0.1	0.1	0.1	—	—	—	—	—
182-275	—	—	—	—	—	—	—	—	—	—	—	—
275-368	—	—	—	—	—	—	—	—	—	—	—	—
368-461	—	—	—	—	—	—	—	—	—	—	—	—
461-554	—	—	—	—	—	—	—	—	—	—	—	—
No./1,000 m³	143	5,402	4,380	2,089	4,018	1,180	874	379	125	18	9	392

TABLE 11.—Vertical distribution (percentage of stage at depth) of larvae and adults of *Euphausia eximia* in day and night samples from the California Current terminus off the mouth of the Gulf of California (Station 10) and number/1,000 m³ in each stage.

			Calyptopis			Furcilia						
Depth (m)	Eggs	Metanauplius	I	II	III	I	II	III	IV	V	VI	Adult
Day:												
0-43	—	—	99.7	99.8	99.9	99.8	99.8	99.3	79.0	33.2	41.2	—
43-136	—	—	0.3	0.2	0.1	0.2	0.2	0.7	21.0	61.8	45.1	—
136-229	—	—	—	—	—	—	—	12.8	14.9	13.5	—	—
229-322	—	—	—	—	—	—	—	—	—	—	7.8	—
322-415	—	—	—	—	—	—	—	—	—	—	—	100.0
No./1,000 m³	—	—	1,021	2,083	3,439	5,522	5,567	1,751	376	382	51	72
Night:												
0-43	—	100.0	100.0	100.0	100.0	99.9	99.8	96.9	93.3	100.0	100.0	72.2
43-86	—	—	—	—	—	0.1	0.2	3.1	6.7	—	—	27.8
86-129	—	—	—	—	—	—	—	—	—	—	—	—
129-222	—	—	—	—	—	—	—	—	—	—	—	—
222-315	—	—	—	—	—	—	—	—	—	—	—	—
315-408	—	—	—	—	—	—	—	—	—	—	—	—
408-501	—	—	—	—	—	—	—	—	—	—	—	—
No./1,000 m³	—	249	79	1,223	3,464	4,260	4,508	1,651	416	150	11	126

TABLE 12.—Vertical distribution (percentage of stage at depth) of larvae and adults of *Euphausia eximia* in day and night samples from the South Equatorial Current (Station 21) and number/1,000 m³ in each stage.

			Calyptopis			Furcilia						
Depth (m)	Eggs	Metanauplius	I	II	III	I	II	III	IV	V	VI	Adult
Day:												
0-37	10.2	—	73.4	58.5	48.1	30.3	11.1	14.1	13.1	28.1	—	—
37-75	41.2	20.6	14.7	31.8	36.9	48.6	56.2	45.7	34.0	—	—	—
75-112	27.5	58.8	—	0.4	—	0.8	7.0	10.5	20.0	—	13.6	—
112-150	20.8	20.1	11.9	9.3	14.7	20.3	25.7	29.7	31.9	34.4	9.1	—
150-227	0.1	0.3	—	—	—	—	—	—	—	—	—	—
227-305	0.2	0.2	—	—	0.3	—	—	—	0.9	37.5	77.3	36.1
305-382	0.1	—	—	—	—	—	—	—	—	—	—	63.9
382-460	—	—	—	—	—	—	—	—	—	—	—	—
No./1,000 m³	35,600	2,184	1,734	2,144	1,285	650	844	1,330	429	32	66	391
Night:												
0-36	21.7	—	25.7	31.9	34.5	35.4	20.4	6.4	16.8	—	19.9	45.1
36-72	20.1	—	59.3	62.1	60.1	51.0	49.1	49.1	50.4	100.0	80.1	39.8
72-108	56.2	98.0	14.1	5.9	5.3	13.3	30.5	43.9	32.8	—	—	15.1
108-144	0.5	—	—	—	—	0.3	—	—	—	—	—	—
144-223	1.4	2.0	0.8	0.1	—	—	—	—	—	—	—	—
223-302	(<0.1)	—	—	—	—	—	—	—	—	—	—	—
302-381	(<0.1)	—	—	—	—	—	—	—	—	—	—	—
381-460	—	—	—	—	—	—	—	—	—	—	—	—
No./1,000 m³	4,478	653	1,605	2,784	2,331	933	407	328	125	25	312	11,388

sinking of calyptopes and early furcilia larvae; almost the entire population remained in the surface layer until furcilia III. Diurnal vertical migration again developed in the last half of the furcilia phase.

The pattern of vertical distribution at Station 21 in the South Equatorial Current (Table 12) had features in common with the distribution observed at Station 6 but was less clearly defined. The position of the calyptopes reflected a developmental ascent from the depth at which eggs had hatched; calyptopis I was more abundant in the surface layer during the day than at night, and there was also some evidence of nighttime sinking in calyptopis II and III. In the furcilia phase the pattern of vertical migration was modified in that the larvae appeared to avoid the surface 0-35 m stratum to some extent. The population structure differed with calyptopis II being the most abundant larval stage.

The differences in larval vertical distribution appeared not to be related to time of sampling; in the upper 150-200 m, where most of the larvae were found, the three night samples were taken between 0000 and 0030 and the day samples in midafternoon (1600) at Stations 6 and 21 and midmorning (0800-0900) at Station 10 (Brinton 1979, figure 3).

DISCUSSION

The species of *Euphausia* were separated into groups, characterized by adult armature of carapace, abdomen, antennule, and petasma, by

Brinton (1975). Among species which have two lateral denticles on the carapace (group IA), *E. eximia* is most closely related to *E. krohnii* and *E. americana* by the conspicuous pectinate dorsal lappet on the first segment of the antennular peduncle. The larvae of *E. krohnii* have been described from the North Atlantic and Mediterranean by Frost (1934) and Casanova (1974) and, while it is not possible to compare the species in detail, the development of *E. eximia* appears to be very similar to that of the North Atlantic population of *E. krohnii*. The timing of acquisition of pigmentation in abdominal photophores may differ; Frost notes that all are pigmented in furcilia III but this condition was not normally seen in *E. eximia* until furcilia V. Development of the distinctive antennular lappet appears to begin at about the same stage (in furcilia V of *E. eximia* at 4.5-5.7 mm TL and in 5.9-6.1 mm larvae of North Atlantic *E. krohnii*) and with variable form. According to Soulier (1963) the lappet of Mediterranean *E. krohnii* develops in a fixed pattern, and >2 spines are not seen until 10 mm TL. There was greater variability in number of telson spines in furcilia IV of *E. eximia*, and one more stage in the furcilia phase, than noted by Casanova (1974) in *E. krohnii* from the Mediterranean. Larvae of the California Current population of *E. eximia* were intermediate in size between the large North Atlantic larvae of *E. krohnii* and the smaller Mediterranean population, while larvae of *E. eximia* from the South Equatorial Current tended to be similar in overall length to Mediterranean *E. krohnii*.

Larval forms appear to be very similar within *Euphausia* species group IA which, besides *E. eximia*, *E. krohnii*, and *E. americana*, includes *E. recurva*, *E. mutica*, *E. brevis*, and *E. diomedeae*. Their larvae share the following characters: spines on anterior margin of carapace in metanauplius, calyptopis phase, and early furcilia stages; a posterodorsal spine on carapace in calyptopis I-III and furcilia I; telson with middle posterolateral spine relatively long until midfurcilia phase; and a fixed pattern of pleopod development which progresses from 1 pair nonsetose to 1 pair setose plus 4 pair nonsetose, and finally to 5 pairs setose pleopods. Talbot (1974) noted variation in number of telson spines developing beneath the cuticle of furcilia III in *E. recurva-mutica* of the Agulhas Current, and Casanova (1974) described timing of events among larvae of *E. brevis* (e.g., modification of antenna and mandible, and development of legs), which is similar to the pattern discerned in *E. eximia*.

Developmental events may vary considerably, however, between the species groups of *Euphausia*. *Euphausia eximia* (group IA) and *E. gibboides* (group IB) differ in several details, some of which are listed in Table 13, although they share all the general features of group IA larvae except pattern of pleopod development. Larvae of *E. gibboides* are larger than those of *E. eximia*, on the average, in the metanauplius and calyptopis phases but they are similar in the furcilia phase due to a slightly higher rate of growth per stage in furciliae of *E. eximia*. The telson is wider in *E. gibboides* from calyptopis I through furcilia I, and the carapace is wider from calyptopis I-III, than in *E. eximia*, with no overlap in range of measurements.

The morphological differences observed within *E. eximia*, between larvae from the California Current terminus and the South Equatorial-Peru Current populations, appear related to the geographical separation of reproductive centers described by Brinton (1979) in his study of the distributional adaptations of euphausiids to the oxygen-deficient eastern tropical Pacific. He found that *E. eximia* achieved the highest densities (>500 beneath 1 m^2) in the South Equatorial Current and across the California Current-eastern tropical Pacific transition off Baja California, the productive zones marginal to the low oxygen waters. The species occurred consistently across a transect of the eastern tropical Pacific but only

TABLE 13.—Some differences in larval development of *Euphausia eximia* and *E. gibboides*.

Feature	*E. eximia*	*E. gibboides*
Pleopods: pattern of development from furcilia I (′ = nonsetose, ″ = setose)	1′ → 1″4′ → 5″	1′ → 1″3′ → 4″1′ → 5″
Telson: dominant pattern of terminal spine reduction from furcilia III to VI	7 → 3/1 → 1 → 1	7 → 5 → 3 → 1
innermost posterolateral spine, inner margin	With spinules	With distal spinule only from furcilia III
number of lateral spines	2 pairs from furcilia V	1 pair
Carapace: stage when anterior median spine develops	Furcilia I	Furcilia V-VI
Antennule: stage when dorsal lappet develops	Furcilia V-VI	Juvenile
Antenna: stage when modified to juvenile form	Furcilia IV	Furcilia V
Mandible: stage when modified to juvenile form	Furcilia IV	Furcilia VI
lateral knob in calyptopis phase	Absent	Present

sparsely (<4 under 1 m²) from lat. 11° to 20° N where the surface temperature exceeded 26° C and lowest middepth O_2 values were <0.05 ml/l through a stratum of 600 m, and where water of westerly origin entered with the Equatorial Countercurrent. Larvae were not observed between lat. 2° and 20° N.

The significant difference in frequency of numbers of lateral telson spines on late furciliae of the California Current and the South Equatorial and Peru Currents may be evidence of the development of reproductive isolation between the two populations. The larval evidence was corroborated by a preliminary survey of adult *E. eximia* which showed a significant difference between populations in the armature of both telson and antennular peduncle. A more thorough examination of adult morphology is necessary, however, for an evaluation of the divergence within the species. The distribution of northern and southern forms observed (Figure 1) suggests that juveniles and adults of *E. eximia* are carried from the species' reproductive center off Baja California into the oxygen-deficient warm waters of the eastern tropical Pacific which may form an effective barrier between the reproductive areas of the two populations.

Variation in size of larvae at the same stage of development (Figure 11) between areas sampled within each population may be related to the amount of food available among other factors. Le Roux (1974), investigating the effects of diet and temperature on the larval development of *Meganyctiphanes norvegica*, demonstrated that rhythm of molt, growth, and morphogenesis were influenced by quality and quantity of food. With excess food, an elevation in temperature caused an acceleration in rate of molt but not precocious differentiation and reduction of the number of larval stages; the larvae were found to be a little smaller in a given stage at the higher temperature due to a decrease in growth per molt.

The relationship of surface temperature to size among *E. eximia* larvae studied was not consistent. Relatively smaller larvae were found at the higher temperature within the South Equatorial-Peru Current population (22° and 16° C at Stations 21 and 1520/1604) but in cooler waters of the California Current (18° and 24° C at Stations 6 and 10). There was a direct correlation of size with abundance of food, however, among California Current larvae; the volume of zooplankton biomass was very low at Station 6 but relatively high at Station 10 (Brinton 1979) reflecting displacement upward of recently upwelled waters with high concentrations of nutrients and probably, with relatively green waters, abundant food for larval forms. The larger size of larvae from Station 10 may also be related to their position in the water column; numbers of calyptopes and early furcilia at Station 6 sank below the surface stratum at night while those at Station 10 remained almost entirely day and night in the food-rich surface layer. Data on biomass and on larval vertical distribution were not available for Stations in the Peru Current for comparison with those in the South Equatorial Current.

Most species of euphausiids studied show indications of some downward daytime vertical migration from calyptopis II (Mauchline and Fisher 1969) but at Stations 6 and 21 (Tables 9, 11) the position of *E. eximia* calyptopes in day and night samples appeared to indicate a reverse pattern of movement. After a presumed developmental ascent from the depths at which nauplii hatched from sinking eggs, the majority of calyptopis I were found in the surface layer in the daytime and in deeper strata at night. The pattern continued through furcilia III at Station 6 and through calyptopis III, to some extent, at Station 21. As noted above, most larvae at Station 10 were found in the surface stratum in both day and night samples through furcilia II; the lack of nighttime sinking in early stages may be related to the shoaling of low oxygen water and upwelling conditions observed in the area (Brinton 1979).

The position of calyptopis I in the day-night series at Stations 6 and 21 suggests that the larvae were drawn to the surface layer by positive phototaxis. Sulkin (1973), working with two species of xanthid brachyurans, showed that, in the absence of light, the distribution of larvae varied with ontogeny; the four zoeal and one megalopa stage assumed a differential vertical distribution due to forces of gravity and hydrostatic pressure as well as different sinking rates, with early stages near the surface. In assessing the influence of light on depth regulation in the same species, Sulkin (1975) suggested that the observed positive phototaxis superimposed a diurnal vertical migration on the basic pattern of differential ontogenetic vertical distribution. Larvae of *E. eximia* appear to show a similar response during the calyptopis phase with modification of their behavior during ontogeny as furcilia develop a pattern of vertical migration similar to that of the adult.

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FEEDING ECOLOGY OF *LAGODON RHOMBOIDES* (PISCES: SPARIDAE): VARIATION AND FUNCTIONAL RESPONSES

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ABSTRACT

Five major ontogenetic stages were found in the diet of pinfish, *Lagodon rhomboides*, from Apalachee Bay, Florida, but diet and dietary breadth showed high degrees of variation with space (both local and geographic), and seasonal variation within size classes was often as dramatic as ontogenetic variation. *Lagodon rhomboides* demonstrated planktivory, omnivory, strict carnivory, and strict herbivory at different times, places, and developmental stages.

Ontogenetic pattern in food habits was primarily a function of mouth size and changing dentition of the predator. Until it reaches 35 mm standard length, the pinfish is an obligate carnivore. Spatial and temporal variation in the food habits of pinfish was a complex function of absolute and relative abundances of food items in the field. Changes in plant consumption by fish larger than 35 mm standard length may be due to changing plant abundance or protection of prey species by macrophyte cover at a given station. Since seagrass biomass and the functional role of a single predator vary over both space and time, plant-animal and predator-prey relationships change continually; however, the life history of *L. rhomboides* is well adapted to seasonal patterns of productivity in food organisms. Multidimensional variation in diets rendered the trophic level concept inoperational. It is concluded that food webs are static neither in time nor in space and that taxonomic species may not be functional components in models of energetic pathways and predator-prey relationships.

In recent years, much research effort has been expended on experiments for testing the role of predation in seagrass meadows (Young et al. 1976; Young and Young 1977, 1978; Orth 1977; Nelson 1978; Reise 1978); yet few experimental ecologists have concerned themselves with variation in the feeding behavior or functional responses of the predators involved in their experiments. The problem is illustrated by empirical data which show the potential for wide variation in the diets of fishes with season (Keast and Welsh 1968; Bell et al. 1978a, b), time of day (Hobson 1974; Hobson and Chess 1976; Robertson and Howard 1978), age or size of the animal (Carr and Adams 1973; Hobson and Chess 1976; Ross 1978), and with locality (Feller and Kaczynski 1975; Love and Ebeling 1978). However, very few scientists have adequately characterized interactions of spatial, temporal, and ontogenetic variations (Keast 1970, 1979; Nakashima and Leggett 1975). Also, field studies that have examined relationships between prey selection by fish and structure of prey assemblages are largely limited to fishes that inhabit structurally simple mud bottom or water column habitats (Feller and Kaczynski 1975; Nakashima and Leggett 1975; Repsys et al. 1976; Stein 1977). To date, only two field studies provide data on the functional responses of fish to prey abundance in seagrass habitats. Robertson and Howard (1978) reported that short-term (diel) dietary shifts in fishes inhabiting beds of *Zostera muelleri* and *Heterozostera tasmanica* were due to vertical movements of holoplankton and facultative zooplankton. Stoner (1979b) showed that the selectivity of prey by pinfish, *Lagodon rhomboides*, was mediated by standing crop of benthic macrophytes. I concluded that increased seagrass biomass resulted in a higher degree of selectivity for certain amphipod species by juvenile fish.

The pinfish is the numerically dominant fish on *Thalassia testudinum* meadows in the shallow subtidal areas of the Gulf of Mexico (Hoese and Jones 1963; Hansen 1969) and on *Z. marina* beds along the Atlantic coast of the United States south of Cape Hatteras, N.C. (Adams 1976). The pinfish is one of the most important predators on macrobenthic organisms of seagrass meadows and has been shown to play a role in the organization of faunal assemblages (Young et al. 1976; Young and Young 1978; Nelson 1978). Data have accumulated on the food habits of pinfish; however, most of the early work reviewed by Caldwell (1957) and

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Carr and Adams (1973) is qualitative and based on small numbers of fish with no particular attention paid to time, space, or fish size. Carr and Adams provided the best published account of food habits of pinfish, noting distinct ontogenetic patterns in the food habits of pinfish and several other fish species which dwell on seagrass beds near Crystal River, Fla. The general conclusion has been that *L. rhomboides* is a generalist feeder. Because *L. rhomboides* is an important mediator of benthic organization, and because the fish is a generalist-type feeder, an investigation was undertaken to test for functional responses of the species to food abundance in the field. Ontogenetic, spatial (local and geographic), and temporal (seasonal) variations in food habits of *L. rhomboides* were explained on the basis of predator morphology, food abundance, and habitat complexity.

METHODS

Based on long-term macrophyte data for the area (Zimmerman and Livingston 1976a, b), four collecting stations were chosen from shallow regions offshore from the mouths of the Econfina and Fenholloway Rivers, in Apalachee Bay, Fla. (Figure 1). One station was located 2.0 km seaward from each of the river mouths and a second was located 4.0 km seaward. Each site was identified with a permanent marker in a location which was representative of a broad area. Stations Econfina 10 and 12 were macrophyte-dominated habitats (primarily *T. testudinum* and *Syringodium filiforme*) with mean annual macrophyte biomasses of 214 and 320 g dry wt/m². The inner station of the Fenholloway area (station 11) was characterized by low macrophyte densities (9.3 g dry wt/m²) and the outer station (Fenholloway 12) was characterized by macrophyte levels (141 g dry wt/m²) intermediate between those levels found at the Econfina stations and those at the inner Fenholloway station (Livingston[2]). All stations were polyhaline with salinities ranging from approximately 17 to 34‰. The mean water depth at all stations was between 1.6 and 2.0 m.

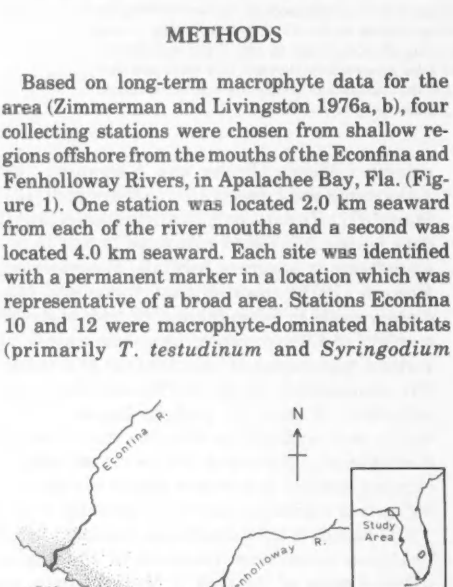

FIGURE 1.—Locations of collecting sites for *Lagodon rhomboides* and food organisms offshore from the Econfina and Fenholloway Rivers in Apalachee Bay, Fla.

Pinfish were collected with a 5 m otter trawl (1.9 cm mesh wing and body, 0.6 cm mesh liner). Seven 2-min tows (2-3 kn) were taken at each station on a monthly basis. The trawling method for the study site was examined by Livingston et al.[3] All tows were made at midday since previous work (Kjelson et al. 1975; Peters and Kjelson, 1975; Adams, 1976) indicated that pinfish feed primarily during daylight hours. All fishes were preserved in 10% Formalin[4]-seawater solution, identified to species, and measured for standard length (SL).

To estimate abundance of prey items in the field, macrobenthic animals (>0.5 mm) and zooplankton were collected on each of the fish collection dates. Macrobenthic prey items were collected with 12 7.6 cm diameter cores and identified to species (Stoner in press). Zooplankton were collected with horizontal tows of a 0.5 m simple conical plankton net with 0.202 mm mesh and a T.S.K. flowmeter. A single tow was made at each station, on each sampling date, at a speed of 1.5 kn. Tow time was dependent upon the abundance of plankton but ranged from 2 to 10 min. Each plankton sample was subsampled with a Folsom plankton splitter when necessary and a 5 ml Hensen-Stemple pipette. One one-hundredth of each sample was counted. Since the importance of planktonic prey items in pinfish food habits was limited to a small part of the population, animals were identified only to major taxonomic group (e.g., calanoid copepod, crab zoea, polychaete larva, etc.)

[2]R. J. Livingston, Associate Professor, Department of Biological Science, Florida State University, Tallahassee, FL 32306, pers. commun. January 1978.

[3]Livingston, R. J., K. L. Heck, Jr., and T. A. Hooks. 1972. The ecological impact of pulp will effluent on aquatic flora and fauna of north Florida: Comparison of a polluted drainage system (Fenholloway) with an unpolluted one (Econfina). Unpubl. Rep., 186 p., to the Coastal Coordinating Council, Florida.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

and the standing crops of each group were calculated.

Plants were quantitatively sampled (Livingston et al. 1976) at the field quadrant from where macrobenthic animals were collected, on the fish collection date. Data on the biomass and species composition of benthic macrophytes at the field stations were provided by Robert J. Livingston.

Fish, macrophytes, and prey animals were collected monthly from November 1976 to December 1977. All collections for a station were made on the same date at midday, and all of the stations were sampled within a 2-4 day period.

For analysis of stomach contents, fish were placed in 5 mm size classes up to 40 mm SL, 10 mm size classes from 40 to 100 mm, and 20 mm size classes for fish >100 mm SL. Food items taken from the stomachs of up to 25 fish in a size class were pooled for each sampling date and station and preserved with 70% isopropanol and a dilute solution of rose bengal stain. The gravimetric sieve fractionation procedure developed by Carr and Adams (1972) was used to analyze stomach contents of pinfish ranging from 11 to 160 mm SL. Stomach contents were washed through a series of six sieves of decreasing mesh size (2.0-0.075 mm mesh) and the frequency of occurrence of each food type was recorded for each sieve fraction. Because all of the items in a particular sieve fraction were of comparable size, the relative proportion of the stomach contents made up of each food type was measured directly by counting. After examination, each sieve fraction was dried overnight at 100° C and the total contribution of each food type was calculated.

With two exceptions, each food particle was placed in a mutually exclusive category. General categories such as amphipod, isopod, harpacticoid copepod, crab zoea, and mysid were employed. The categories animal remains (unidentified tissue stained with rose bengal) and plant remains were the only food categories that were not mutually exclusive from other groups. Plants specifically identified were *T. testudinum* and *S. filiforme*. The general food categories, 40 in number (Table 1), were used for statistical analyses; however, whenever an animal or plant could be identified to a more specific group (e.g., family, genus, species) this information was recorded.

Cluster analysis, employing the similarity coefficient, ρ (Matusita 1955; Van Belle and Ahmad 1974), and flexible grouping cluster strategy ($\beta = -0.25$) was used to describe ontogenetic variation in food habits of *L. rhomboides*. The appropriateness of the cluster strategy for dealing with fish diet data was discussed by Sheridan (1978).

TABLE 1.—List of the general food categories encountered in the stomachs of pinfish and the codes employed in food habit histograms.

Code	Food category	Code	Food category
AM	Amphipod	IS	Isopod
BA	Barnacle	IT	Invertebrate tube
BI	Bivalve	MY	Mysid
BR	Branchiuran	NE	Nematode
BZ	Bryozoan	NM	Nemertean
CC	Calanoid copepod	NU	Nudibranch
CH	Chaetognath	OS	Ostracod
CR	Crab	PL	Polychaete larvae
CU	Cumacean	PM	Plant matter
CZ	Crab zoea	PO	Polychaete
DE	Detritus	SA	Sand
DI	Diatom	SC	Scallop
FE	Fish egg	SH	Shrimp
FL	Fish larvae	SL	Spicule
FO	Foraminifera	SP	Shrimp postlarvae
FR	Fish remains	SY	*Syringodium filiforme*
GA	Gastropod	TA	Tanaid
HC	Harpacticoid copepod	TH	*Thalassia testudinum*
HY	Hydroid	VL	Veliger larvae
IE	Invertebrate egg		
MS	Miscellaneous — used in food habit histograms for all food items making up <3% of the total mass.		

Stepwise multiple regression was used in certain instances to analyze the relationships between amounts of food items consumed by pinfish and abundance of food items in the field. Dependent variables included the amount of amphipod, shrimp, and plant material in stomachs (percent of contents in dry weight) and independent variables were amphipod, shrimp, plant, calanoid copepod, and polychaete abundance values. Maximization of the coefficient of determination, r^2, was the criterion for selecting the best multiple regression model. The minimum F value for inclusion of variables in the regression equations was set at 0.01.

RESULTS

Nearly 5,000 pinfish, representing 61% of all trawlable ichthyofauna in Apalachee Bay, were collected at four field sites during a 1-yr sampling period. The number of fish collected at a station, however, was a direct function of the mean macrophyte biomass at the site ($r = 0.998$, $P>0.01$). Most of the fish were collected between April and October (Figure 2).

The stomach contents of 2,174 pinfish taken from the four field sites were analyzed. Although the unvegetated site (Fenholloway 11) produced only 82 pinfish in routine trawl collections, over 600 stomachs of fish from each of the vegetated

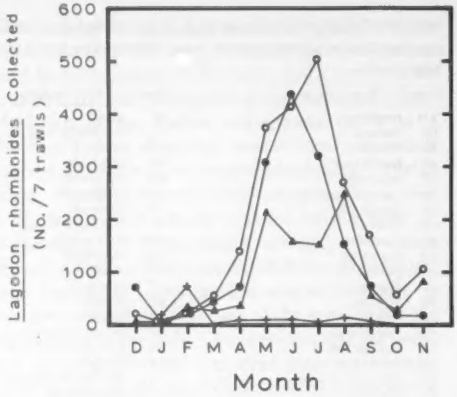

FIGURE 2.—Number of *Lagodon rhomboides* collected in Apalachee Bay, Fla., from December 1976 to November 1977. Crosses = Fenholloway 11, triangles = Fenholloway 12, dots = Econfina 10, circles = Econfina 12.

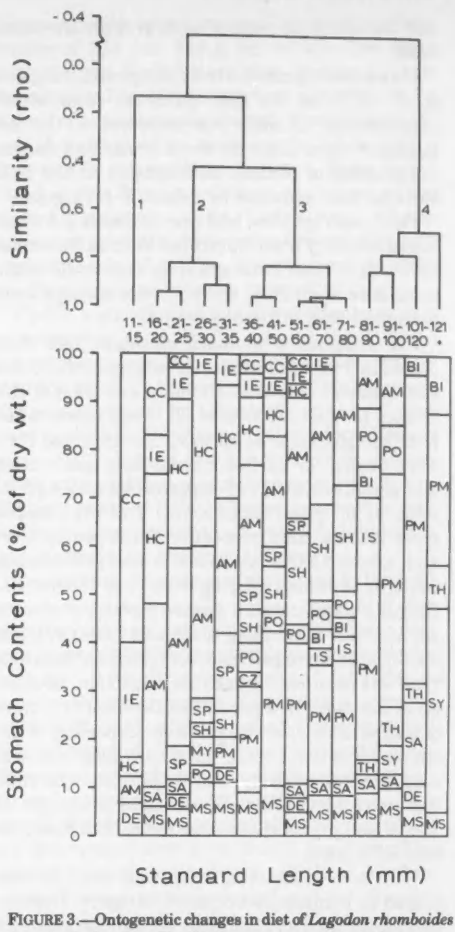

FIGURE 3.—Ontogenetic changes in diet of *Lagodon rhomboides* from Apalachee Bay, Fla. Histograms represent relative proportions of major dietary components (dry weight). Dendogram represents cluster analysis of diet similarity among size classes. Codes for the food items are given in Table 1. (See text for explanation of the cluster strategy.)

stations were examined. The relative proportions of various food items taken by pinfish of different size classes (for all dates and stations) varied widely with fish size (Figure 3) and cluster analysis showed four distinct ontogenetic trophic groups. The first group was planktivorous and includes only those fish <16 mm SL. The second group (16-35 mm) included fish which took harpacticoid copepods and amphipods in nearly equal proportions plus small amounts of shrimp postlarvae, invertebrate eggs, and other animals. This group was largely carnivorous. Fish of group three (36-80 mm) were omnivores, taking about 30% of their diet in the form of plant material (mostly microepiphytes) and the rest from the macrobenthic fauna (mainly amphipods, small shrimp, and some harpacticoid copepods). Group four (>80 mm) included mostly adult fish, >1 yr old. At least one-half of the diet was plant material; however, stomach contents of fish >100 mm SL were <10% animal matter. A large portion of the plant matter consumed was seagrass, especially *S. filiforme*.

Pinfish diet was dependent upon the place of capture as well as size of the fish (Table 2). Although a large percentage of the stomachs were empty, the primary food item of pinfish between 11 and 15 mm SL was calanoid copepods at Fenholloway 11, Fenholloway 12, and Econfina 12. Fish of the same size class took a large number of invertebrate eggs at the inner stations, Econfina 10 and Fenholloway 11. Harpacticoid copepods and amphipods were important food items only at Econfina 10. The percentage of diet made up by calanoid copepods was directly related to the mean calanoid copepod standing crop (number per cubic meter) at a given station and time ($r = 0.804$, $P<0.05$) (Figure 4). No significant relationships were found between amphipods consumed by the small pinfish and abundance of amphipods in the field; however, amphipods were consumed by post-

TABLE 2.—Composition of stomach contents of *Lagodon rhomboides* at four stations in Apalachee Bay, Fla. Each value is the mean percentage of the total dry weight of stomach contents for the fish size class indicated.

Item	Fen 11	Fen 12	Econ 10	Econ 12
	SL = 11-15 mm			
n (% empty)	23(70.0)	10(70.0)	35(42.8)	28(42.8)
Calanoid copepods	58.1	91.9	17.3	79.7
Invertebrate eggs	23.9		47.7	8.8
Detritus	18.0	8.1		4.3
Harpacticoid copepods			19.0	2.3
Amphipods			16.0	4.9
	SL = 16-35 mm			
n (% empty)	14(14.3)	140(5.0)	213(1.4)	235(2.1)
Harpacticoid copepods	7.0	40.8	26.5	38.3
Amphipods	30.0	18.3	38.5	28.3
Invertebrate eggs	9.5	8.0	2.7	7.3
Shrimp postlarvae	3.0	6.0	13.5	7.5
Polychaetes		2.8	1.7	1.0
Plant matter		2.9	2.5	4.2
Shrimp	3.0	5.3	1.5	0.2
Calanoid copepods	40.0		1.0	5.2
Miscellaneous	7.5	15.9	12.1	8.0
	SL = 36-80 mm			
n (% empty)	35(8.6)	380(6.6)	460(3.0)	408(4.4)
Amphipods	56.8	27.2	27.2	30.1
Plant matter	16.5	25.3	30.0	23.0
Harpacticoid copepods	0.8	5.6	6.4	6.0
Shrimp postlarvae	0.8	2.8	4.2	1.4
Shrimp	1.3	12.3	9.7	17.7
Polychaetes	3.3	5.0	2.5	5.2
Calanoid copepods	3.3	2.9	2.6	3.6
Invertebrate eggs	0.8	3.5	2.9	5.0
Bivalves		3.7	0.4	
Miscellaneous	16.4	11.7	14.1	8.0
	SL > 80 mm			
n (% empty)	10(30.0)	85(15.3)	78(11.5)	20(15.0)
Plant matter	6.0	63.3	84.3	91.7
Polychaetes	0.7	4.9	0.1	
Amphipods	6.0	8.1	2.4	2.0
Bivalves	81.3	10.1	0.4	
Miscellaneous	6.0	13.6	12.8	6.3
Total number	82	615	786	691
% Empty	29.3	8.4	5.2	5.5

larval fish at Econfina stations 10 and 12 only. The small epifaunal amphipod *Gitanopsis tortugae*, one of the few species consumed by small pinfish, was collected only at these two stations during these months (see Stoner (1979a) for a detailed analysis of prey species consumed by *L. rhomboides*). Because no data are available on abundance of harpacticoid copepods in Apalachee Bay, the importance of their abundance to food habits of pinfish remains unknown.

The main components of the diets of pinfish between 16 and 35 mm were amphipods, harpacticoid copepods, and shrimp postlarvae at the three vegetated sites; amphipods and calanoid copepods at Fenholloway 11. Shrimp and shrimp postlarvae were abundant at the vegetated stations, but few in number at the unvegetated site (Table 3). This probably explains the differences in shrimp consumption. Calanoid copepods were apparently substituted for shrimp at Fenholloway 11, although the copepods were less abundant at that site than at other stations (Econfina 10 and 12) between April and July (Table 3). Low abundance of harpacticoid copepods may explain their relatively low contribution to the food habits of young pinfish at the unvegetated site.

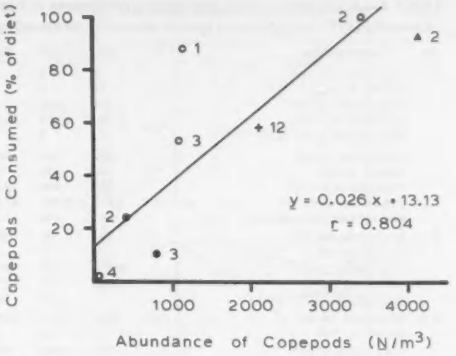

FIGURE 4.—Percentage of stomach contents (dry weight) of postlarval pinfish composed of calanoid copepods shown as a function of copepod abundance in Apalachee Bay, Fla. Cross = Fenholloway 11, triangle = Fenholloway 12, dots = Econfina 10, circles = Econfina 12. Months are indicated by numbers beside the plotted points.

Diets of fish from 36 to 80 mm were similar at the three vegetated stations and included large amounts of amphipod, shrimp, and plant material. At the unvegetated site, amphipods made up approximately twice the percentage found in fish from vegetated stations. Because of low shrimp abundance at the unvegetated site, shrimp contributed little to the diets of fish inhabiting that site. Amphipods appear to have been substituted for shrimp.

Fish >80 mm demonstrated wide variability in the percentage of the stomach contents composed of plant material, ranging from 6.0% at Fenholloway 11 to 91.7% at Econfina 12. The diet of fish from the unvegetated station was dominated by the mussel *Brachidontes exustus*. For adult fish, the mean percentage of the diet composed of plant material was a direct function of the mean standing crop of benthic macrophytes at a given station ($r = 0.952$, $P<0.05$); however, there was wide temporal variation in the standing crop of benthic macrophytes at the vegetated sites (Table 3) which was not followed by proportional changes in plant consumption at Econfina 10 and Fenholloway 12.

TABLE 3.—Abundance of prey organisms and biomass of benthic macrophytes[1] in Apalachee Bay, Fla., from December 1976 to November 1977. Only epifaunal species commonly consumed by *Lagodon rhomboides* were included in the abundance of amphipods.

Stn	Prey organisms	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
F 11	Amphipods, no./m²	95	0	38	189	114	0	152	0	0	95	152	151
	Shrimp, no./m²	19	0	0	0	0	19	19	38	38	0	19	0
	Polychaetes, no./m²	171	246	719	908	1,834	794	284	416	739	701	361	1,287
	Copepods, no./m³	2,144	4,423	3,469	946	659	0	327	2,232	4,651	2,583	1,576	1,775
	Macrophytes, g dry wt/m²	—	3	1	6	5	5	8	11	16	10	20	18
F 12	Amphipods, no./m²	379	246	152	245	1,209	397	479	246	454	794	730	1,493
	Shrimp, no./m²	57	38	38	0	94	38	190	19	341	133	76	57
	Polychaetes, no./m²	1,948	1,194	1,436	1,325	1,722	2,005	1,477	701	965	1,760	607	2,460
	Copepods, no./m³	1,973	5,935	4,182	2,202	81	109	411	796	2,730	3,123	1,792	686
	Macrophytes, g dry wt/m²	—	110	152	96	197	70	145	165	175	243	117	84
E 10	Amphipods, no./m²	114	76	359	870	1,133	2,910	1,514	416	1,720	567	302	1,846
	Shrimp, no./m²	19	0	19	19	19	0	95	189	114	114	208	208
	Polychaetes, no./m²	1,154	663	1,079	814	569	2,119	910	758	907	853	625	2,947
	Copepods, no./m³	1,020	543	385	803	1,981	7,130	1,069	4,042	3,404	2,898	1,315	1,227
	Macrophytes, g dry wt/m²	—	96	164	58	230	246	216	234	279	392	319	126
E 12	Amphipods, no./m²	926	1,191	2,230	1,190	813	1,512	1,000	624	339	435	549	1,343
	Shrimp, no./m²	76	19	19	38	76	0	57	57	95	38	76	0
	Polychaetes, no./m²	946	1,665	1,304	1,097	890	1,553	1,062	815	797	683	380	1,156
	Copepods, no./m³	807	1,147	3,440	1,070	0	527	258	1,387	3,447	2,745	2,136	948
	Macrophytes, g dry wt/m²	—	259	237	118	240	319	456	390	374	619	401	104

[1]Macrophyte data were provided by R. J. Livingston (see text footnote 2).

This point will be discussed later. Polychaetes, bivalves, amphipods, and other taxa were consumed by adult pinfish where macrophyte cover was low.

Seventy percent of the postlarval pinfish from Fenholloway stations were empty and 42.8% of the fish from Econfina stations had no stomach contents (Table 2). Empty stomachs in pinfish >15 mm SL were less common than found in postlarval fish, but fish collected at the unvegetated site consistently had the highest percentage of empty stomachs. Between 11.5 and 15.3% of adult fish taken from vegetated sites had empty stomachs, but 30% of the adults from Fenholloway 11 were empty.

Ontogenetic and spatial variations in pinfish diet were interrelated with changes in diet with season. Overall diet of the pinfish population at a given station was highly dependent upon the length-frequency composition of the population (Figure 5); therefore, to examine independently the effect of season on food habits, size was held constant. Individual size groups, based on the cluster analysis of feeding ontogeny (Figure 3) were tested for seasonality in diet. Although the mean length of fish in the 16-35 mm SL size class increased from 20 to 32 mm between March and August, an analysis of dietary changes within 5 and 10 mm size classes indicated that the bias was not serious and that the change in food habits over time within the larger size group was an accurate representation of dietary seasonality. Length-fre-

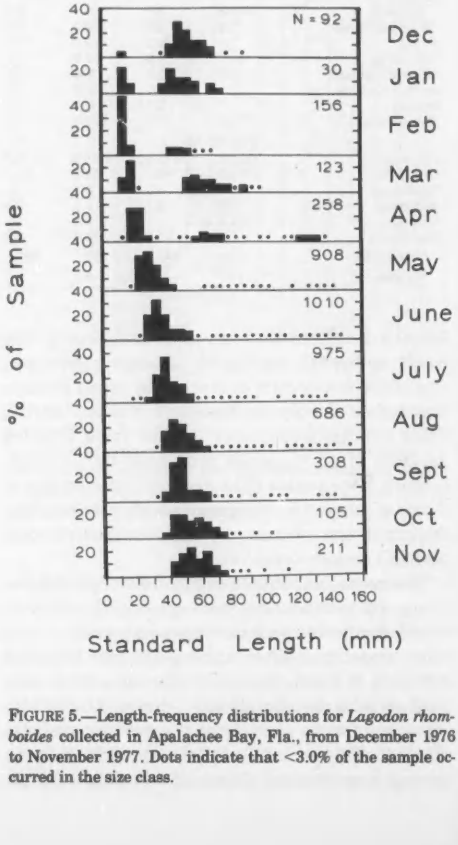

FIGURE 5.—Length-frequency distributions for *Lagodon rhomboides* collected in Apalachee Bay, Fla., from December 1976 to November 1977. Dots indicate that <3.0% of the sample occurred in the size class.

quency changes related to season within the 36-80 mm and adult size groups were minor. Because of insufficient data for the site, Fenholloway 11 was eliminated from analysis of seasonal variation in pinfish diet.

Data were sufficient for seasonal analysis of diet in postlarval pinfish only at Econfina 12. Pinfish <16 mm SL were collected at this site from January through April. In January and February, postlarval pinfish consumed primarily calanoid copepods, plus a small number of invertebrate eggs. Later, they consumed harpacticoid copepods and amphipods in large quantities, and no calanoid copepods were taken by postlarvae in April. The relative abundance of calanoid copepods and invertebrate eggs in the diet of these fish coincided directly with the absolute abundance of the planktonic food items as determined by plankton tows taken on the day of fish collections. Copepods and invertebrate eggs were most abundant in January and February, and declined to annual lows in April (Table 3). Amphipod abundance remained relatively high at Econfina 12 through the winter and spring with annual minima occurring in the fall. Because amphipods were most abundant in January and February (Table 3), when copepod consumption was highest, it would appear that calanoid copepods are the preferred prey of postlarval pinfish. Only when calanoid populations fell to near zero did amphipods become a major portion of the diet.

Pinfish of the carnivorous feeding group (16-35 mm SL) were collected from March through August. In the spring and summer, amphipods and harpacticoid copepods were the primary dietary components of these fish (Figure 6). Clearly, however, amphipods were most important at Econfina 10. Amphipod consumption decreased with time and by late summer the primary dietary components were harpacticoid copepods and small shrimp. A small amount of plant material was taken at all three vegetated stations in midwinter. Invertebrate eggs and other animal foods consistently contributed small amounts to the diets of pinfish between 16 and 35 mm SL.

Temporal variations in diet of pinfish from 16 to 35 mm were analyzed by stepwise multiple regression using calanoid copepod, shrimp, amphipod, and benthic macrophyte abundance (Table 3) as independent variables. Amphipod consumption was positively correlated with amphipod abundance (except Econfina 10) and negatively related to plant, shrimp, and calanoid copepod abundance.

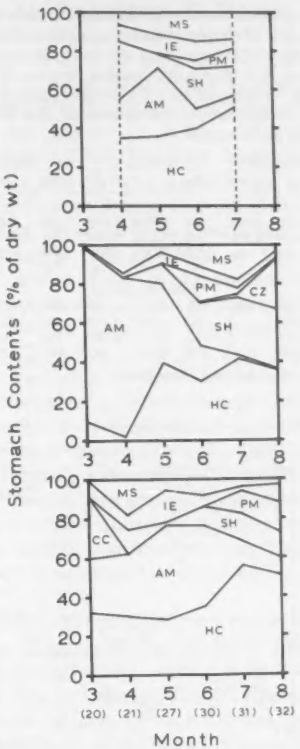

FIGURE 6.—Seasonality in diet of *Lagodon rhomboides* between 16 and 35 mm SL from three stations (F 12-top, E 10-middle, E 12-bottom) in Apalachee Bay, Fla. (March to August 1977). Diet is given as the relative proportion of the dry weight of stomach contents. Codes for the dietary components are given in Table 1. Numbers in parentheses are the mean lengths of fish.

At least 97.6% of the variation in amphipod consumption was explained by three independent variables for all three stations. Significant multiple correlation values for temporal variation in shrimp consumption were obtained for fish from Econfina 10 and 12 (r^2 = 0.986 and 0.999, respectively) (Table 4). Shrimp consumption was positively correlated with shrimp abundance, plant biomass, and calanoid copepod abundance. Negative relationships were found with amphipod abundance. Harpacticoid intake was positively related to plant biomass.

Pinfish between 36 and 80 mm SL were available year-round at vegetated sites and were considered to be omnivores. Examination of temporal

TABLE 4.—Pearson correlation coefficients (r) and coefficients of determination (r^2) for percentages of total stomach contents (dry weight) composed of: amphipods and shrimp in *Lagodon rhomboides* from 16 to 35 mm SL, tested as functions of food abundance. AM = amphipods/m², CC = calanoid copepods/m³, PM = grams dry weight benthic macrophytes/m², and SH = shrimp and shrimp postlarvae/m².

Fenholloway 12			Econfina 10			Econfina 12		
Step	r	r^2	Step	r	r^2	Step	r	r^2
			Amphipods consumed					
CC	-0.909	0.826	SH	-0.802	0.643*	AM	0.887	0.787*
SH	-0.234	0.995*	AM	-0.083	0.994**	SH	-0.716	0.866*
AM	0.482	n.s.	CC	-0.388	0.999**	PM	-0.090	0.976*
PM	-0.391		PM	-0.692	n.s.	CC	-0.792	n.s.
			Shrimp consumed					
CC	0.789	n.s.	SH	0.872	0.760*	AM	-0.825	0.681*
SH	0.318		AM	-0.066	0.972**	CC	0.231	0.868*
AM	-0.741		CC	0.257	0.986*	PM	0.662	0.998**
PM	-0.056		PM	0.604	n.s.	SH	0.783	n.s.

*$P \leq 0.05$; **$P \leq 0.01$; n.s. = not significant.

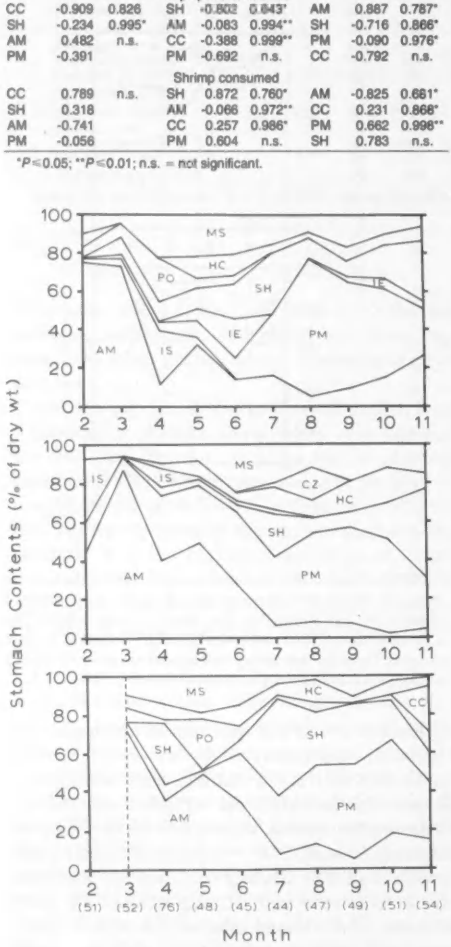

FIGURE 7.—Seasonality in diet of *Lagodon rhomboides* between 36 and 80 mm SL from three stations (F 12-top, E 10-middle, E 12-bottom) in Apalachee Bay, Fla. (February to November 1977). Diet is given as the relative proportion of the dry weight of stomach contents. Codes for the dietary components are given in Table 1. Numbers in parentheses are the mean lengths of fish.

variation in the diet of this ontogenetic group, however, showed that plant material made up only a small portion of the diet in winter and early spring (Figure 7). Amphipod consumption was highest in March and decreased through the spring and fall, during which time plant material became the most important food item. Consumption of shrimp and shrimp postlarvae was low in the spring but increased to as much as 30% of the diet in the summer and fall. Consumption of calanoid copepods by this fish size class was generally limited to winter. Harpacticoid copepods consistently contributed a small amount to the diet of these fish but consumption of isopods, crab zoea, and polychaetes was sporadic.

For fish from 36 to 80 mm, temporal variations in consumption of amphipods, plant matter, and shrimp were analyzed with stepwise multiple regression, using abundance of shrimp, amphipods, polychaetes, and benthic macrophytes as independent variables. Pearson correlation coefficients show that consumption of amphipods was negatively correlated with abundance of shrimp and macrophytes in the field and positively related to amphipod abundance (Table 5). The relationships with polychaete abundance were mixed. Multiple correlation coefficients explained between 60.8 and 79.4% of the temporal variation in amphipod consumption using from two to four independent variables. Consumption of plant matter by fish from 36 to 80 mm was positively related to plant biomass and shrimp abundance.

TABLE 5.—Pearson correlation coefficients (r) and coefficients of determination (r^2) for percentages of total stomach contents (dry weight) composed of: amphipods, plant matter, and shrimp in *Lagodon rhomboides* from 36 to 80 mm SL, tested as functions of food abundance. AM = amphipods/m², PO = polychaetes/m², PM = grams dry weight benthic macrophytes/m², and SH = shrimp and shrimp postlarvae/m².

Fenholloway 12			Econfina 10			Econfina 12		
Step	r	r^2	Step	r	r^2	Step	r	r^2
			Amphipods consumed					
SH	-0.561	0.315	SH	-0.802	0.643**	AM	0.616	0.380
AM	-0.462	0.500*	PM	-0.588	0.746**	SH	-0.126	0.664*
PO	0.105	0.608*	PO	-0.090	0.758*	PM	-0.574	n.s.
PM	-0.448	0.631*	AM	0.126	0.794*	PO	0.524	
			Plant matter consumed					
SH	0.639	0.408*	PM	0.912	0.831**	PO	-0.714	0.510
AM	0.105	n.s.	SH	0.594	0.912**	SH	0.214	0.652*
PO	-0.257		PO	-0.304	0.926**	AM	-0.694	0.786*
PM	0.428		AM	0.022	0.955**	PM	0.635	n.s.
			Shrimp consumed					
PO	-0.034	n.s.	PO	0.654	0.428*	PM	0.496	n.s.
AM	0.316		AM	0.013	0.667*	SH	-0.116	
PM	-0.218		SH	0.389	0.698*	AM	-0.388	
SH	0.024		PM	-0.401	0.741*	PO	-0.197	

*$P \leq 0.05$; **$P \leq 0.01$; n.s. = not significant.

Plant consumption was inversely related to polychaete field density at all three stations and relationships with amphipod abundance were mixed. Multiple regression did not provide a satisfactory model for variation in plant matter consumed at Fenholloway 12, but plant and food item abundances explained 78.6 and 95.5% of the variation at Econfina 12 and 10. Explanation of temporal variation in shrimp consumption by multiple regression methods was successful only for fish from Econfina 10 ($r^2 = 0.741$). Shrimp intake increased with shrimp abundance in the field and decreased with plant and polychaete abundances. Other correlations were low. Harpacticoid copepod consumption was positively related to plant biomass and negatively correlated with amphipod abundance; however, multiple correlation coefficients were not computed since no data were available on harpacticoid abundance.

Diet of large pinfish (>80 mm SL) showed little seasonality at Econfina 10, where plant material made up at least 80% of the stomach contents on all dates. At Fenholloway 12, however, benthic vegetation was less abundant than at Econfina 10 and major changes in diet occurred with season (Figure 8). Clearly, large pinfish were carnivorous during winter and early spring at Fenholloway 12, but became herbivorous in May. Winter diet included polychaetes, bivalves, amphipods, and isopods. Animal material was unimportant in the diets of fish taken during the rest of the year.

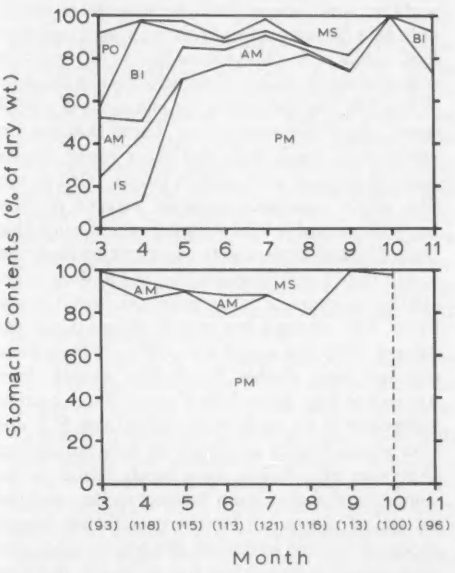

FIGURE 8.—Seasonality in diet of *Lagodon rhomboides* >80 mm SL from two stations (F 12-top, E 10-bottom) in Apalachee Bay, Fla. (March to November 1977). Diet is given as the relative proportion of the dry weight of stomach contents. Codes for the dietary components are given in Table 1. Numbers in parentheses are the mean lengths of fish.

Temporal variation in the diets of adult fish was not adequately explained with multiple regression, as obvious trends in plant consumption did not follow seasonal patterns in macrophyte abundance. Lack of temporal variation in diet at Econfina 10 is due to the fact that plants were readily available at that station when adult pinfish were present (March through October). On the other hand, at Fenholloway 12, macrophytes were patchy in distribution and a high biomass in April (Table 3) was composed largely of *T. testudinum* which was generally not consumed by pinfish. Abundance of alternative prey organisms, such as isopods and bivalves, may also explain carnivory of adult pinfish at Fenholloway in the spring.

Breadth of diet in pinfish was examined by calculating Shannon-Weiner diversity indices, H', and by tabulating the number of food items that individually contributed >1.0% of the total mass of stomach contents for each fish size class, sampling date, and station (Table 6, Figure 9). Dietary diversity of pinfish between 16 and 80 mm was lowest at the unvegetated site because two food items, amphipods and calanoid copepods, overwhelmed the importance of other foods. Low abundance of alternative prey such as shrimp, shrimp postlarvae, and benthic macrophytes probably explain this occurrence. For fish >80

TABLE 6.—Dietary diversity, H', and number of food types (individually contributing >1.0% of the total mass of stomach contents) in *Lagodon rhomboides* from four stations in Apalachee Bay, Fla. (mean ± SD). Within a fish size group, no mean values were significantly different (ANOVA and Duncan's multiple range test, $P>0.05$).

Size group (mm)	Fen 11	Fen 12	Econ 10	Econ 12
		Dietary diversity, H'		
11-15	—	—	0.57±0.39	0.54±0.64
16-35	0.99±0.50	1.68±0.17	1.28±0.59	1.45±0.13
36-80	1.27±0.46	1.68±0.44	1.64±0.44	1.58±0.25
>80	—	0.92±0.44	0.50±0.36	0.41±0.22
		Number of food types		
11-15	—	—	2.2±0.9	2.7±2.0
16-35	5.0±2.8	7.5±2.1	5.5±2.3	5.8±1.2
36-80	6.2±1.7	8.6±2.4	8.1±3.0	7.2±1.2
>80	—	6.2±2.3	4.4±1.7	4.5±0.7

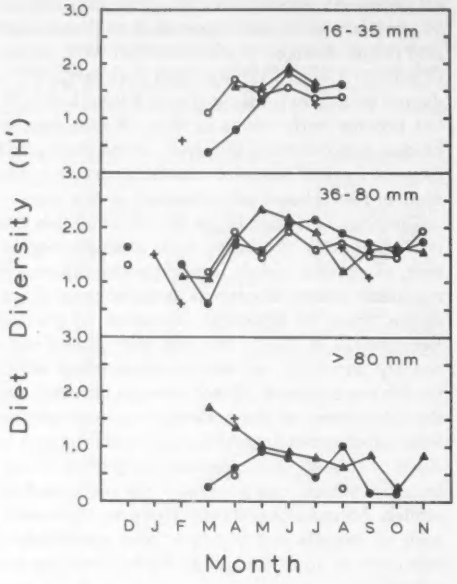

FIGURE 9.—Breadth of diet in *Lagodon rhomboides* from four sites in Apalachee Bay, Fla., shown as a function of season. Each value is the Shannon-Weiner index, H', for the food items consumed by fish of three size classes. Crosses = Fenholloway 11, triangles = Fenholloway 12, dots = Econfina 10, circles = Econfina 12.

mm, dietary diversity was highest at the sparsely vegetated station because, in addition to plant material, mussels, polychaetes, and other animal prey made an important contribution to the diet. At the Econfina stations, the diets of adult fish were dominated by plant material causing low dietary diversity.

Pinfish between 36 and 80 mm SL showed greatest breadth in diet; however, some degree of seasonality in dietary diversity occurred in all fish >15 mm (Figure 9). In fish between 16 and 35 mm, peak dietary breadth in June and July corresponded with periods of low amphipod abundance and a change in food habits to alternative prey types including shrimp and plant material. Lowest dietary breadth in fish between 36 and 80 mm occurred in the late winter and spring when amphipods were abundant and macrophyte biomass was low. Diversity of food items available was probably lowest at this time. Dietary diversity in fish >80 mm SL reflected the degree of carnivory by the fish. At Fenholloway 12 dietary diversity was highest in March and April when various animal foods were consumed in large quantities. At Econfina 10, highest diversity occurred in August when a large number of animal foods supplemented a normally herbivorous diet. During late spring and summer months, dietary diversity indices at Econfina 10 and Fenholloway 12 converged to similar values as fish at both stations became largely herbivorous. Very low dietary diversities occurred at Econfina 10 in September and October because over 98% of the diet was composed of plant material.

DISCUSSION

Pinfish from Apalachee Bay passed through five major ontogenetic feeding stages, including 1) planktivory; 2) carnivory on amphipods and harpacticoid copepods; 3) omnivory on amphipods, shrimp, and microepiphytes; 4) omnivory on epiphytes, amphipods, polychaetes, and isopods; and 5) herbivory on epiphytes and vascular plant material (primarily *S. filiforme*). Darnell (1958) and Carr and Adams (1973) provide the most reliable data for comparison with the present study on food habits of *L. rhomboides* since each provided information on ontogenetic variation in the diets of the fish. Darnell, studying stomachs of pinfish from Lake Ponchartrain, La., found that the importance of amphipods and other small crustaceans decreased with pinfish length (40-150 mm SL), while vegetable material became increasingly important in diet with fish size. Except that Darnell found dipterans to be a common food item in fish from Lake Ponchartrain, his findings were similar to mine. Pinfish collected near Crystal River, Fla., showed five trophic stages (Carr and Adams 1973); the stages were different from those reported here (Table 7). Unlike pinfish from Apalachee Bay, those from Crystal River became herbivores at an early stage (36-60 mm SL), and later showed strict carnivory on fish and shrimp (>80 mm SL). Fishes were rarely found in the stomachs of pinfish from Apalachee Bay and the pattern of increasing herbivory with fish length appeared to hold except at the unvegetated site where plant material was not available. Because stomach analyses for both geographical areas covered a full year, differences between the findings of the two studies cannot be attributed to artifacts introduced by seasonal variation in diet. Rather, it is likely that different abundances of suitable prey or plant items explain geographical differences in

TABLE 7.—Trophic ontogeny of pinfish collected at Crystal River and Apalachee Bay, Fla. Crystal River data were taken from Carr and Adams (1973).

Feeding stage	Size of fish (mm SL)
Crystal River	
1. Planktivore on copepods	10- 20
2. Carnivore on shrimp, mysids, and amphipods	28- 30
3. Herbivore on epiphytes	38- 60
4. Omnivore on epiphytes, shrimp, and fish	61- 80
5. Carnivore on shrimp and fish	81-110
Apalachee Bay	
1. Planktivore on copepods and invertebrate eggs	11- 15
2. Carnivore on amphipods and harpacticoids	16- 35
3. Omnivore on amphipods, harpacticoids, shrimp, and epiphytes	36- 80
4. Omnivore on epiphytes, amphipods, polychaetes, and isopods	81-120
5. Herbivore on epiphytes and vascular plants	>120

food habits just as food abundance explained local variations in food habits among stations in Apalachee Bay. Carr and Adams described their study site as dominated by *Ruppia maritima* and *Halodule wrightii*. In Apalachee Bay, benthic vegetation was dominated by *T. testudinum*; therefore differences in food habits of pinfish between the two areas, may be due to characteristics of the habitat other than prey abundances. For example: 1) the wide blades of *T. testudinum* may provide better refuge from predation for shrimp and other crustaceans than that provided by narrow blades of *R. maritima* and *H. wrightii*, and/or 2) the plant material near Crystal River was, in some way, unsuitable as food for large pinfish. Hansen (1969) also reported that plant material was the dominant food item of pinfish from dense *Thalassia* and *Ruppia* beds in Pensacola Bay, Fla., suggesting that some characteristic of *Thalassia* beds promotes herbivory in pinfish. Similar to the present study, Hansen found that seasonal variation in plant consumption was related to seasonal availability of benthic macrophytes.

Trophic ontogeny in pinfish can be explained in terms of fish morphology. Width and height of the mouth in the open position was linearally related to standard length of pinfish and increased body and mouth size permitted pinfish to capture a broader range of prey sizes (Stoner 1979a). The same characteristics undoubtedly explain increases in numbers of prey types associated with increasing body size in juvenile fish. Increasing range of prey sizes and types with fish body and mouth size has been reported by many authors (e.g., Wong and Ward 1972; Ware 1972, 1973; Ross 1978). Transition to herbivory by pinfish, first as a microepiphyte nibbler and later to a seagrass grazer is associated with changes in dentition with growth. Very fine conical jaw teeth only are found in fish at 15 mm SL, but conical teeth are replaced by longer caninelike teeth in fish between 23 and 35 mm. Conical and canine teeth are well adapted for capturing small animal prey, but chisel-shaped incisors, which appear in fish >35 mm, provide pinfish with the dentition required to graze plant material. Because of its dentition, the pinfish is probably an obligate carnivore until it reaches about 35 mm SL (for further discussion and illustration of ontogeny in pinfish dentition, see Caldwell 1957).

Given the morphological constraints of *L. rhomboides*, its reproductive seasonality is particularly well adapted for exploitation of food resources in seagrass meadows of Apalachee Bay. Postlarval pinfish entered the seagrass beds in midwinter at the time of peak abundance of calanoid copepods, appropriately small prey organisms. Winter spawning placed juvenile fish (16-35 mm) on the seagrass beds in the spring when the most valuable prey species, amphipods and harpacticoid copepods, were beginning to reproduce and reaching maximum abundance (Stoner[5]; Thistle[6]). Optimal prey for larger pinfish (36-80 mm) probably includes larger organisms such as shrimp which had peak abundance in the fall. Reproductive timing and growth placed large pinfish on the grass beds in the fall. The life history strategy of *L. rhomboides*, therefore, appears to be adapted to seasonal patterns of productivity and abundance in prey and macrophyte species. Although pinfish were among the fishes that were shown to influence the abundance of zooplankton in the Newport River estuary (Thayer et al. 1974), it is unlikely that pinfish postlarvae affect the abundance of calanoid copepods in Apalachee Bay because of the low number of pinfish postlarvae in the shallow bay (Brady 1980). However, pinfish probably do regulate the abundance of certain amphipod species in the bay (Stoner 1979a, b).

Variation in food habits with space, both on local and geographic scales, was a function of food availability and habitat structure. Food habits of fishes in Apalachee Bay were dramatically different at stations separated by distances as little as 2

[5]Stoner, A. W. 1980. Abundance, reproductive seasonality, and habitat preferences of amphipod Crustacea in seagrass meadows of Apalachee Bay, Florida. Manuscript in review.

[6]D. Thistle, Assistant Professor, Department of Oceanography, Florida State University, Tallahassee, FL 32306, pers. commun. December 1978.

km. At the station where vegetation and epibenthic prey organisms were sparse, pinfish took more food from the water column (e.g., copepods, chaetognaths, and polychaete larvae) than at other stations. Due to the lack of vegetable matter at this station, pinfish consumed *Brachidontes exustus* which lives on oyster bars near the unvegetated site. A high percentage of empty stomachs at the unvegetated site indicates that feeding conditions there were poor, especially for postlarval and adult pinfish. Although selection of food by fish is confounded by food preferences, the consumption of food by pinfish appears to reflect local, geographic, and seasonal abundances of the food organisms and the morphological limitations of the consumer.

Temporal variations in the food habits of *L. rhomboides* were well explained by abundance of prey types in the field, but the correlations were complex. Amphipod, shrimp, and plant consumptions were all directly related to the abundance of these primary food items in the field. Seasonal relationships between food abundance and consumption by fishes were observed by Lawler (1965), Repsys et al. (1976), and Hickey (1975). Diurnal changes in food habits have also been explained by changes in prey availabilities (Hobson and Chess 1976; Robertson and Howard 1978). Keast's (1970) observation that close correlation of prey availability with seasonality in food habits holds for only the most important prey types was also observed in this study. For example, polychaetes were relatively minor components of pinfish diets and showed no correlation with seasonal abundance patterns. On a statistical basis, however, absolute abundance of a food item in Apalachee Bay explained only part of the variation in consumption of that item. For example, although amphipod consumption by juvenile pinfish was directly related to amphipod abundance in the field, amphipod intake was also inversely related to shrimp and plant abundances. These inverse relationships were often stronger than the positive relationship with amphipod abundance. Similarly, shrimp consumption was negatively correlated with amphipod and plant abundances, suggesting that the relative abundance of preferred prey items may be as important as absolute abundance of any one type. The picture is further clouded by the fact that plant material, which serves as an important food source for pinfish >35 mm, is also an obvious component of the habitat that lends protection to many small prey species (Nelson 1978; Stoner 1979a). Two explanations for the increased plant consumption with benthic macrophyte biomass are plausible: 1) plant material is taken as a simple response to its abundance, and/or 2) *T. testudinum* blades provide amphipods, shrimp, and other animal prey with protection from fish predation and inhibit the consumption of these animals; therefore, as blade density or plant biomass increases, macrophytes and epiphytes are taken as alternative food. Both mechanisms are probably influential in the determination of food habits in pinfish; however, the latter hypothesis is probably the most important mechanism since cellulase activity is not found in the alimentary tract of *L. rhomboides* (Stickney and Shumway 1974). Densely vegetated seagrass habitats support greater densities and biomass of potential prey species than unvegetated or sparsely vegetated substrates (O'Gower and Wacasey 1967; Orth 1977; Brook 1978; Stoner in press), although is is unknown as yet whether this relationship is due to reduced predation on the animals or some property inherent in the structure of the habitat. The problem of omnivory in pinfish would be an especially fertile area for investigation in terms of optimal foraging theory, but a large array of carefully controlled field and laboratory experiments would be required.

Dietary specialization is generally found to be correlated with increasing food abundance. This conclusion is supported by models of predator-prey relationships (see review by Pyke et al. 1977) and empirical studies with fishes (Ivlev 1961; Zaret and Rand 1971; Werner and Hall 1974). On the basis of seasonal prey abundance patterns and the diets of pinfish between 16 and 80 mm SL, dietary specialization did occur with periods of high prey abundance. For example, at the vegetated stations amphipods and other macrobenthic organisms were most abundant between February and May. Lowest dietary diversities occurred during the same time period. With adult fish, however, the characteristic relationship did not seem to hold. Fenholloway 12 and Econfina 10 showed similar seasonal trends in abundance of food organisms yet seasonality of dietary diversity was entirely different at the two stations. Also, on a spatial basis, lowest dietary diversity occurred at the site with extremely low food abundance (Fenholloway 11) for fish between 16 and 80 mm SL. More generalized diets were found at the vegetated sites where food was more abundant. The predicted relationship of increasing dietary specialization

with increasing food abundance did not hold in certain instances because the abundance of macrobenthic organisms at the study site was closely related to standing crop of benthic macrophytes at the site (Stoner in press). Also, since seagrasses and epiphytes serve as important dietary components of larger pinfish, prediction of dietary diversity is further complicated.

Data provided in this study further verify the conclusion that *L. rhomboides* is a generalist feeder. Schoener (1969) suggested that generalist feeding strategy is favored when: 1) food density is low and there is a premium on the ability of the animal to take a range of prey, 2) the predator has a relatively long period to gain energy, and 3) prey densities fluctuate widely. Given the relatively low abundance of prey species in Apalachee Bay, the great diversity of potential prey items, and their high degree of variability with time and space, the generalist feeding strategy exhibited by *L. rhomboides* would be predicted by Schoener's model.

The detailed analysis of the food habits of *L. rhomboides* provided in this study accentuate difficulties inherent in the description of a trophic niche. Because of dramatic variation in food habits and dietary breadth in coastal fishes, serious methodological problems arise in description of food habits. In most cases, length-frequency distributions of fish are not constant with time; consequently, when animals are not placed in size classes or when placed in overly large size classes, dietary variation may be due to either seasonal changes in food habits or increasing fish size. The diet of a group of fish will be a function of the length-frequency distribution of the population if variation with size occurs. When food habits are examined by size and not by season, variation within a given size class may appear greater than is actually true at any particular time, and seasonality of diet is completely obscured. Variability in food habits as a function of space (a common occurrence) adds still one more dimension to the problem of describing an animal's food and feeding habits, but spatial variation is usually ignored. Keast (1970), in a study of the bioenergetic interrelationships of cohabiting freshwater fishes in Ontario, provided insight into the complex interactions of fish size and season in determining food habits. One other study (Nakashima and Leggett 1975), an investigation of responses of yellow perch to different levels of phytoplankton and benthic biomass in Lake Memphremagog, Quebec-Vermont, showed interactions of time and fish size in diet determination. The dimension of space was added by comparing the diets of fish from the northern and southern basins of the lake. Few studies have described more than one dimension of an animal's food habits.

Peters (1977) stated that the "Trophodynamic Concept" (Lindeman 1942) is based upon the premise that organisms in an ecosystem are categorized according to their distance along a food chain from the sun. He pointed out, however, that the real world is constructed of complex food webs and organisms do not fall into neat categories such as "primary consumer" or "secondary carnivores." This is not a new idea. In 1961, Darnell asserted that "trophic level" is an inoperational term since: 1) animals of a given size and belonging to a single species take food from several sources, 2) alternate foods are frequently utilized as a function of their availabilities, 3) an ontogenetic progression of food habits is common in animals, and 4) many animals are dependent upon detrital material which is itself of a complex origin and an undefined distance from primary producers. Regier and Henderson (1973) and Kercher and Shugart (1975) provided similar reasoning for the inadequacies of the trophic level concept. Darnell recommended a spectral approach to the food habit problem and Kercher and Shugart defined an "effective trophic position," actually a continuous index of trophic position rather than the conventional discrete level. Neither solution to the problem addressed all of Darnell's objections and gave an accurate portrayal of the functional role of the organism in its ecological context. Data provided in this paper show that, in addition to ontogenetic pattern in food habits, animals within given size classes take foods from several sources with the possible exception of postlarval pinfish which are collected only in the winter and early spring. Fish of many size classes consumed significant quantities of calanoid copepods which are probably herbivores; harpacticoid copepods which may be detritovores, herbivores, or carnivores; amphipods which show wide variety in food habits; plus shrimp, invertebrate eggs, and many other invertebrate taxa. In most cases, the prey species themselves cannot reliably be placed in any one trophic level and, since individuals of a given species were consumed at different developmental stages, and prey species may show trophic ontogeny, the problem of assigning a trophic level to the predator is further

confounded. Pinfish >35 mm SL nearly always contained both plant and animal material in their stomachs. Omnivory, of course, automatically makes the fish both a "primary" and "secondary consumer." Darnell's (1961) suggestion that predators commonly utilize food resources according to their availabilities was clearly demonstrated in this paper as it related to other spatial and temporal patterns of food abundance in Apalachee Bay. Although pinfish do not rely directly on detrital material as a source of nutrition, many of its prey organisms do (e.g., certain harpacticoid copepods, amphipods, shrimps, and polychaetes). Because it is difficult to place detritovores in trophic levels, the predatory fish also falls within no discrete level. On these bases, the trophic level concept is rendered inoperational for relationships involving the dominant epibenthic fish in Apalachee Bay. Furthermore, because of migration of consumers and wide variation in food habits with season and consumer growth, one may never assume that food webs, predator-prey relationships, or the functional role of a predator are static. The taxonomic species is not, in many cases, a functional ecological unit. At the very least, ontogenetic feeding groups should be incorporated in ecological models. These "trophic units" would be particularly useful where the true ecological role of the animal in a model is important. Except in the most simple food webs, without precise knowledge of variation in food habits and diet breadth, models of energetic pathways and predator-prey relationships and measurement of niche breadth and overlap will be accurate neither in theory nor in practice.

Characteristics of prey species which mediate predation include absolute and relative abundances, conspicuousness, size, palatability, defensive morphology and behavior, spatial distribution including microhabitat and aggregation, and nutritional value. All of the above, however, are limited or mediated by various elements of the environment including temperature, turbidity, dissolved oxygen, light, water motion, and structural aspects of the habitat. Although a great deal of research has been conducted concerning the importance of predator and prey characteristics, most of the work has been done in structurally simple systems, including mud bottom, freshwater pond, and water column habitats where the number of food species is relatively low. Data from this and another paper (Stoner 1979b) show that seagrass blades and rhizomes provide a very important structural component in seagrass meadows which affect both predator and prey species and their interactions. Since seagrass biomass, blade densities, and species compositions vary over both time and space, plant-animal and predator-prey relationships are in constant flux. The seagrass habitat, therefore, is an extremely complex system within which the ecological roles of predation and habitat structure are ever changing. The need for further investigation is obvious.

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OBSERVATIONS ON A MASS STRANDING OF SPINNER DOLPHIN, *STENELLA LONGIROSTRIS*, FROM THE WEST COAST OF FLORIDA

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ABSTRACT

The spinner dolphin, *Stenella longirostris*, while well known in portions of the Pacific Ocean, has rarely been available for study in the Atlantic. Data from 28 individuals from a mass stranding in Florida enabled us to make preliminary estimates of mean size and age at sexual and physical maturity, reproductive seasonality, and sexual dimorphism for this species in the southwest Atlantic. Our sample most closely resembles the Hawaiian populations described by Perrin, but further work in the Atlantic is likely to demonstrate other populations differing morphologically from this one.

The spinner dolphin, *Stenella longirostris*, is widely distributed in tropical to warm temperate waters of the world (Perrin 1975), but due to its predominately pelagic habits, is seldom found stranded and is not generally taken in coastal fisheries. As a result, very little is known of its biology except in the eastern tropical Pacific, where it is taken in considerable numbers incidental to purse seining for yellowfin tuna. Perrin et al. (1977) have recently published investigations on the eastern population of spinner dolphin from the Pacific.

The species is apparently common in the Caribbean (Caldwell et al. 1971; Erdman et al. 1973; Taruski and Winn 1976), but there are few records, all of them strandings, from the Gulf of Mexico. Gunter (1954) did not find any evidence of this species in the Gulf of Mexico. Layne (1965) reported on a mass stranding of this species from Dog Island, Fla. (lat 29°48′ N, long. 84°38′ W), where 36 animals stranded on September 1961. Lowery (1974) reported a single adult male from Fort Walton Beach, Fla. (lat. 30°24′ N, long. 84°47′ W). Schmidley and Shane[5] reported a 158 cm male which stranded alive at Sabine Pass Beach, Tex., on 16 May 1976, and a pregnant 188 cm female found on Padre Island, Tex., during March 1975. Shane (1977) reported two additional records from Padre Island: a 173 cm female which stranded about January 1976 and a 183 cm male on 4 June 1977. The present study is based on 28 animals from a single mass stranding on the west coast of Florida.

At this point it is not possible to determine whether the occurrences recorded from the west coast of Florida were derived from a population in the Gulf of Mexico or were strays from the Caribbean. While there is a small fishery for mixed species of dolphins in the Caribbean (Caldwell et al. 1971), catches of spinner dolphin are relatively infrequent and are unlikely to have an appreciable effect on the population. In contrast, the populations studied by Perrin and others in the Pacific are taken in large numbers incidental to purse seining for yellowfin tuna.

The causes of mass strandings of cetaceans are still very little understood (see Geraci 1978 for a recent review of the subject). It is clear that this is a very complex problem which goes far beyond the scope of this paper. It is also clear that much of our lack of understanding is based upon a lack of information on the species involved. We have felt that it was also important to include material on the circumstances of the stranding itself, even though this is not directly related to the conclusions drawn from examination of the specimens.

CIRCUMSTANCES OF THE STRANDING

The stranding occurred on the north end of Casey Key, with most of the dolphins concentrated

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[5]Schmidley, D. F., and S. H. Shane. 1978. A biological assessment of the cetacean fauna of the Texas coast. Final Rep., U.S. Marine Mammal Commission Contract MM4AC008, available Natl. Tech. Inf. Serv., Springfield, Va., as PB 281763, 38 p.

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at about lat. 27°12′10″ N, long. 82°30′30″ W (Figure 1). The animals began coming ashore about 2200 h e.d.t. on the evening of 13 July 1976. At that time the wind was westerly at 10-15 mi/h, seas were running about 2 ft, and there was an extreme low tide at 2211 h. Upon discovering the animals, local residents attempted to direct them back to sea or move them to more sheltered areas.

Most observers concurred that there was a great deal of noise coming from all of the dolphins when they first came ashore, including much "squealing and crying," but that this later subsided. The animals were quite passive on the beach, with the exception of one large animal that reacted violently to handling and died during the short trip to Midnight Pass. Most of the dolphins did not resist handling and were easily walked to the shallow sand bar 10-15 m from shore, where they were pointed seaward, held until they began rhythmic swimming motions, and then given a push offshore. This was believed to be successful with some of the animals, but in many cases they would turn towards the south with the first wave that came over the bar and be washed back onto shore.

Eight to 10 animals, one of which was marked on the dorsal fin with a cattle ear tag, were moved to the more sheltered waters of Midnight Pass and released in there. A single small animal (possibly 504457)[6] was released in Little Sarasota Bay. The last live animal to come ashore with the initial stranding was 504449 which was found at 0130 h and died while attempts were being made to direct it back to sea. Estimates of the total number of animals ranged from 50 to 150, with most of the observers agreeing on the lower number.

Early morning of 14 July, four large animals and a calf stranded just north of Turtle Beach on Siesta Key, about 2 km north of the original stranding. Three of the large animals were directed back to sea, one died on the beach and was subsequently lost, and the calf (504459) was moved to Turtle Lagoon where it died. All of the live animals were off of the beach by 0800 h.

Later that morning, two live animals were picked up, one from the northeast end of Casey Key along the Intracoastal Waterway, and one from the grass beds just east of Bird Keys. The animal which had been tagged the night before (504434) was recovered dead from the latter area. Both of the live animals were probably from the group that had been transported and released at Midnight Pass. The live animals were held in an impoundment at the Mote Marine Laboratory on Siesta Key until they were picked up by Sea World and transported to holding facilities at Orlando, Fla., on 15 July. One of these (504456) died the next day; the other (504455) died 4 days later. A dead calf (504458) was recovered from the southern tip of Siesta Key, a dead adult (504451) was picked up on the west side of Bird Keys, and the accumulation of dead animals at the original stranding site on Casey Key was recovered and put on ice at the Mote Marine Laboratory on 14 July.

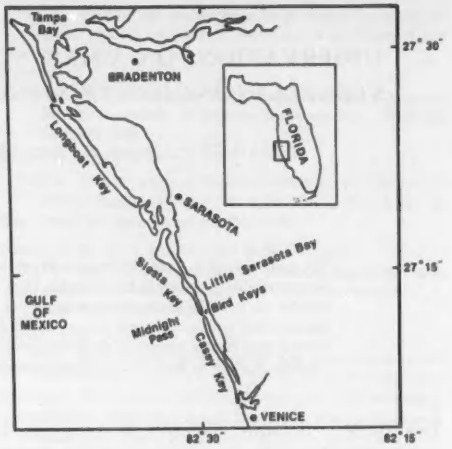

FIGURE 1.—Central west coast of Florida localities involved in the mass stranding of spinner dolphin.

Late afternoon of 15 July, we received notification that a small dolphin had been seen in the Intracoastal Waterway near marker no. 23 about 6 km south of Midnight Pass. This animal (504457) was found just after dark swimming slowly near shore and whistling loudly. It was picked up alive, but died early the next morning while being transported to Orlando. This was probably the calf which had been released in Little Sarasota Bay on 13 July.

The last animal to be recovered was the decomposed carcass of an adult male that was picked up on 16 July from Casey Key (504460).

An aerial survey was flown in a U.S. Coast Guard helicopter from 1800 to 2000 h on 14 July and on the afternoon of 16 July. No animals other than the dead ones on the beach were seen. The

[6]The six digit numbers used to identify the animals are catalog numbers of the United States National Museum, where the skeletal remains have been deposited.

stranding received a great deal of publicity from the news media, and it would be expected that we would have been notified if any additional animals had turned up on the coast.

Most of the dolphins bore minor abrasions that were probably incurred while stranding. Only one (504448) exhibited any appreciable physical damage. This animal, the largest male of the group, had two large shark bites on the left flank at about midlength and a third which completely removed the left fluke. These bites appeared to have been inflicted after death.

NECROPSY

One specimen was necropsied late on the evening of 14 July, the others on 15 July. The two animals which were transported to Sea World were necropsied on 16 and 20 July by the Sea World staff. A variety of lesions were observed in the sample necropsied on 15 July. Most were parasitic and not serious enough to account for death. The blubber layer appeared thin, but this was due at least in part to postmortem changes in the hot sun and measurements were not taken.

The stomachs of all specimens except the three calves were empty. Nicholas Hall (Department of Neuropathology, University of Florida, Gainesville, FL 32601) collected the brains from the animals necropsied on 15 July for neuropathological examination. Helminth parasites were collected and forwarded to Donald Forrester (Laboratory of Wildlife Disease Research, University of Florida, Gainesville, FL 32611). Gonad samples were collected and later analyzed at the Smithsonian Institution by Mead. Teeth were taken from all of the animals except the calves and were sectioned at about 175 μm in thickness by Odell using a Buehler Isomet Low Speed Saw[7], and were read for age determination by Odell and Mead. External measurements were taken by Wells and Scott while the animals were still on the beach, and organ weights were taken during the necropsies. Copies of all the measurements and necropsy data are in the Marine Mammal Program files (Division of Mammals, Smithsonian Institution, Washington, DC 20560). Skeleton materials from the specimens are being studied by William F. Perrin (Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038).

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

REPRODUCTIVE DATA

The female reproductive tracts were removed, flat diameter of uterine horns measured at their midlength, ovaries collected and fixed, uterus opened and examined for fetuses, and mammary glands checked for gross indications of lactation. The ovaries were examined for externally visible corpora, indications of large maturing follicles, and were weighed. The ovaries were subsequently sectioned by William F. Perrin, providing confirmation of the external examination and an exact count of the corpora albicantia. None of the animals were visibly pregnant and only one (504456) was lactating. For practical purposes, females were considered sexually mature if there were external indications of at least one corpus on the ovaries. There was only one individual (504440) in which there was a discrepancy between the results of the external ovarian examination and the sectioning (Table 1). In this case a large follicle was probably mistaken for a corpus albicans on external examination.

The smallest sexually mature female was 187 cm long, and the largest immature female was 190 cm long. A 177 cm female showed no indications of follicular development, while four animals between 180 and 186 cm showed external indications of maturing follicles. The diameter of the larger of the two uterine horns showed a considerable increase (about twofold) at sexual maturity.

The good correspondence between ovarian condition and diameter of the uterine horns indicates that the latter may be a useful character for defining sexual maturity, as it is probably the result of pregnancy.

It seems likely that females begin to mature at about 180 cm and reach sexual maturity at a length of about 188 cm and a weight of about 55 kg. The 188 cm pregnant female reported by Schmidley and Shane (see footnote 5) fits this interpretation.

Considering only those females in which the pulp cavity of the tooth was open and for which an exact count of growth layer groups[8] could be made, there were four sexually immature animals, with a mean of 8.25 growth layer groups (7, 8, 8, and 10 groups), and three sexually mature animals, with a mean of 10 groups (7, 11, and 12 groups). Al-

[8]Terminology adopted at International Workshop on Determining Age of Odontocete Cetaceans, 8-19 September 1978, Southwest Fisheries Center, NMFS, NOAA, La Jolla, Calif.

TABLE 1.—Reproductive data on female spinner dolphin stranded in Florida. Epiphyses: 0 = open; 1 = closed; 2 = fused. Sexual maturity: 0 = mature; 1 = maturing; 2 = mature. Ages are in number of dentinal growth layer groups with + signifying that the pulp cavity was closed and the age was greater than the number of visible groups. The right and left ovaries were confused on 504437. However, they are presumed to correspond to the relative diameter of the uterine horns.

USNM number	Length (cm)	Weight (kg)	Age	Epiphyses	Gonad weight (g)		Uterine diameter (cm)		Ovarian corpora		Sexual maturity
					Right	Left	Right	Left	Right	Left	
504438	177	49	10	0	0.81	0.76	1.5	1.5	0	0	0
504450	180	54	8	0	0.48	1.47	1.5	1.5	0	0	1
504449	181	46.1	7	0	0.45	1.36	1.4	1.5	0	0	1
504453	183	47.5	8	0	0.50	1.08	1.5	1.5	0	0	1
504454	186	54	7	0	0.29	1.02	1.2	1.2	0	0	1
504441	187	55.3	8+	0	1.16	4.29	2.0	2.8	0	4	2
504444	189	53	11+	0	0.37	1.58	1.8	1.3	0	0	1
504440	190	56	7	0	0.81	1.85	1.3	1.6	0	0	1
504437	195	61.1	12	0	0.95	6.3+	1.9	3.0	0	1	2
504433	196	60.3	6+	1	1.39	1.99	1.9	2.3	0	7	2
504445	197	64	—	0	1.57	2.46	1.6	2.0	0	1	2
504451	201	65.2	11	2	1.22	5.11	2.9	3.0	0	9	2
504456	204	59	—	—	1.55	4.5	—	—	—	—	2

though sample size is small, it gives a useful preliminary estimate of age at sexual maturity of 7-10 growth layer groups (7-10 yr, see Perrin et al. 1976, 1977 for discussion of alternative growth layer-age relationships).

Comparable figures were given by Perrin et al. (1977) for the eastern spinner dolphin from the Pacific. They found a mean length at sexual maturity of 165 cm which is appreciably shorter than the estimate for this sample (188 cm). This is due at least in part to the eastern spinner dolphin being a relatively smaller animal (mean length of sexually mature females was 171 cm, whereas it was 197 cm for this sample). Perrin et al. (1977) found that mean age at sexual maturity was 5.5 growth layer groups, which may represent a decrease in age at sexual maturity as a result of fishing pressure on the eastern spinner population. This also might contribute to the shorter length at sexual maturity in that population.

As appears to be the case with many delphinids, there was a marked dominance of the left side of the reproductive tract (Harrison et al. 1972). In all of the mature or maturing animals, the left ovary was decidedly larger than the right, and only one animal (504441) bore any externally visible corpora on the right ovary. There was a corresponding asymmetry in the size of the uterine horns, with the left being equal to or larger than the right in all but one animal (504444), indicating that the greater number of pregnancies were carried in the left horn.

The testes were measured, weighed with the epididymis removed, and a sample taken for histological examination. Sections of testis samples were cut at 10 μm, stained with hematoxylin and eosin, and the diameter of the seminiferous tubules measured with an ocular micrometer. The tubules were randomly selected for examination, but only those approaching a direct rather than an oblique cross section and free from obvious artifacts of sectioning or decomposition were chosen for measurement. The least diameter was measured and the results given in Table 2 are the mean of 10 tubules, at a depth of about 1 cm from the surface of the testis. Tubules were also mea-

TABLE 2.—Reproductive data on male spinner dolphin stranded in Florida. Epiphyses: 0 = open; 1 = closed; 2 = fused. Sperm in epididymis: 0 = none; 1 = present; 2 = copious. Testis activity: 0 = no spermatogenesis; 2 = active spermatogenesis. Sexual maturity: 0 = immature; 1 = maturing; 2 = mature. Ages are in number of dentinal growth layer groups, with + signifying that the pulp cavity was closed and the age was greater than the number of visible layers.

USNM number	Length (cm)	Weight (kg)	Age	Epiphyses	Gonad weight (g)		Gonad length (cm)		Sperm in epididymis	Testis activity	Tubule diameter	Sexual maturity
					Right	Left	Right	Left				
504434	188	51	7	0	18	17	11	10	0	0	62	0
504435	189	55.8	7	0	250	220	24	20	0	1	136	1
504455	190	63.6	8+	—	320	310	—	—	1	—	—	1
504439	192	65.5	9+	1	730	720	32	30	—	1	244	2
504436	194	65.3	10	0	400	430	23	24	2	1	185	2
504442	195	60	10	—	—	460	27	27	1	1	180	2
504443	197	68	9+	1	560	550	27	25	1	1	200	2
504447	197	63.8	7+	0	96.5	100	15	16	1	0	80	0
504446	201	75	9+	2	860	870	31	32	2	1	196	2
504452	203	63.6	9+	—	500	500	27	27	1	1	173	2
504448	208	69+	8+	1	980	870	36	35	2	—	—	2

sured near the surface of the testis and it was noted that tubule diameter averaged about 10% less at that level in the mature males. The process of selection of the tubules for measurement may have introduced a slight bias in favor of smaller tubules, as these are possibly less likely to have been affected by decomposition artifacts. Much of the variation in tubule diameter within an individual slide may have been the result of autolytic distortion, which would tend to increase the diameter of the tubules.

There is a sharp increase in the size of the testes of animals with length of 188 or 189 cm (Table 2), which apparently is the size range at which maturation of the testes begins. Spermatogenesis was taking place in the testes of the 189 cm individual, but the testes weights were still low relative to those of fully mature animals and no sperm was present in the epididymis. In the next largest animal (190 cm), the testes were slightly larger and sperm was present in the epididymis, indicating that this animal was functionally sexually mature. All of the animals above 190 cm had large, active testes and were sexually mature, with the exception of a single 203 cm individual (504452), whose testes were markedly small, though there was a slight indication of spermatogenesis. The body weight of this animal was also low for its length, and it is probable that it was an abnormal individual.

Although the sample of males was too small to statistically define sexual maturity, it seems likely that maturation begins around a body length of about 190 cm and a weight of about 60 kg, and maturity is reached at a length of about 192 cm and a weight of about 65 kg. Animals with a seminiferous tubule diameter of less than about 150 μm were immature or maturing, and those with a diameter in excess of this were sexually mature. The corresponding figures for testis weight and length were about 300 g and 24 cm. The sample of males with the pulp cavity open in the teeth consists of only four specimens. One of these did not have well-defined growth layers, leaving only three usable individuals. These are an immature animal with 7 growth layer groups and two mature animals with 10 groups.

Perrin et al. (1977) found a mean length at sexual maturity of about 175-180 cm (the middle of several estimates based on different criteria, and the estimate which is most comparable with that applied to the present sample) and a mean age at sexual maturity of about 10-12 groups in the eastern spinner dolphin. As was seen when comparing the sexual maturity figures for females from the two populations, the eastern spinner reaches maturity at a shorter length than our sample from the Gulf of Mexico. In the case of males, the ages at attainment of sexual maturity are more similar and the length difference is probably due to population differences in mean size of individuals.

PRODUCTIVE SEASONALITY

Of the six mature females in this sample, one (504456) was lactating and one had a large corpus luteum with no visible conceptus. Both of these had probably given birth recently. None of the six were pregnant. Six of the seven mature males were examined for presence of sperm in the epididymis. Sperm was present in all six and was judged to be copious in three. Admittedly, this is a very small sample, but it is indicative of recent calving and breeding activity.

Perhaps the most convincing evidence for recent reproductive activity in this sample are the three calves which were present, with lengths of 90, 91, and 97 cm. Perrin et al. (1977) estimated length at birth in the eastern spinner to be 75.5 cm. Since the mean lengths of mature animals and the mean lengths at attainment of sexual maturity in the Florida sample are uniformly about 14% greater than the corresponding figures for the eastern spinner dolphin, it is logical to assume, for an initial approximation, that length at birth would also be about 14% greater, or about 86 cm. Perrin et al. (1977) estimated the postnatal growth rate in the first 10 or 11 mo after birth to be 4.77 cm/mo. Again, allowing a difference of 14% for the larger mean size in the Florida sample, a usable estimate of the growth rate during this period would be 5.4 cm/mo. This provides projected ages for the two smaller calves of about 1 mo old, and for the larger of about 2 mo, with birth dates of mid-June and mid-May.

The only other data available for spinner dolphins in the Gulf of Mexico are the 8.1 cm fetus which Layne (1965) found in an animal which stranded in mid-September and the 61 cm fetus which Schmidley and Shane (see footnote 5) found in early March. Using the fetal growth curve for the eastern spinner (Perrin et al. 1977), and assuming that the mean size difference between the populations would not be significant for small fetuses, the approximate date of conception for the

8.1 cm fetus would be late June or early July, and for the 61 cm fetus would be early May.

Thus, although the data are few, there is a convincing consistency indicative of a calving season for this population in early summer (May-July).

PHYSICAL MATURITY

Physical maturity was judged on the basis of examination of the epiphyseal suture in one of the midthoracic vertebrae and noting whether a cartilaginous plate was present (open), absent but with the epiphyseal line still visible (closed), or absent with all trace of the epiphyseal suture obliterated (fused). The suture was examined on a cut surface at least 1 cm deep, and generally on a median section of a whole centrum. Closure of the suture takes place last along the periphery of the epiphyseal plate, and a shallow cut can frequently be misleading. As can be seen in Table 2, males reached physical maturity at about the same size as sexual maturity (with the exception of 504447, which as noted earlier, was probably an abnormal individual). Females, however, reached physical maturity considerably after sexual maturity, at a length of about 196 cm and a weight of about 61 kg.

EXTERNAL MORPHOLOGY

External measurements were taken in the manner outlined by Norris (1961), at the time the animals were picked up from the beach, using a steel tape graduated in centimeters. Numbers in parentheses in the text refer to the numbered measurements as defined in that paper. In the following discussion, relative dimensions are with respect to the total length of the individual, and are expressed as the means of the individual dimensions divided by the individual total lengths (Table 3). Figure 2 shows the long slender rostrum and a pigmentation pattern characteristic of this species.

Sexual dimorphism in the external measurements was most apparent in the relative length of the rostrum (snout to apex of melon (3)). This dimension was about 7% larger in females for the total sample, but was less in the adult and neonatal samples. Perrin (1975) found the same sexual difference in the sample of *S. longirostris* which he examined from the Pacific.

The other anterior body measurements which are taken from the tip of the snout show sexual differences of a lower relative magnitude, due to inclusion of the rostral length as a component of these dimensions. We should then expect, if no other factors were active, that all measurements containing rostral length would be proportionately greater in females, and all those not containing rostral length would be proportionately smaller. In this particular sample, however, the variation is such that these differences are not apparent in most cases.

TABLE 3.—External measurements on Florida spinner dolphin expressed as individual dimensions divided by individual total lengths. For these purposes animals with a total length >195 cm were considered adult. Numbers in parentheses refer to Norris (1961) for definitions of the measurement.

Measurement	Sample	*N*	Mean	SD
Snout to apex of melon (3)	Total males	12	0.089	0.005
	Total females	14	.095	.008
	Adult Males	9	.090	.005
	Adult females	4	.093	.005
	Neonatal males	1	.080	—
	Neonatal females	2	.081	.005
Snout to genital slit (13)	Adult males	9	.652	.020
	Adult females	5	.706	.023
Girth at anus (23)	Adult males	9	.312	.012
	Adult females	5	.281	.022
Fluke width (34)	Total males	12	.233	.017
	Total females	15	.216	.017
	Adult males	9	.235	.019
	Adult females	5	.222	.016
	Neonatal males	1	.221	—
	Neonatal females	2	.210	.014
Height of dorsal fin (32)	Total males	12	.102	.009
	Total females	15	.095	.006

The position of the center of the genital slit, as determined by the measurement from the tip of the snout to the genital slit (13), differs between males and females, with the center of the slit being farther posterior in females. The difference amounts to a relative increase of about 8% in this measurement in adult females when compared with adult males. This particular sexual difference seems to be true of cetaceans in general.

Girth at the anus (23) relative to total length is about 11% greater in adult males. This is correlated with development of a postanal keel in adult males as described by Perrin (1972, 1975).

The relative width of the flukes (34) was 5-8% greater in males in the adult, total, and neonatal samples. Although the variation in this character renders this statistically insignificant in this sample, the same sort of difference was found by Perrin (1975) in his Pacific samples, suggesting that it is a real difference. The relative height of the dorsal fin (32) was 7% greater in males in the total sample. Here again, the variation renders the difference statistically insignificant. There is a possible indication that the flippers are relatively larger in females, but the difference is slight

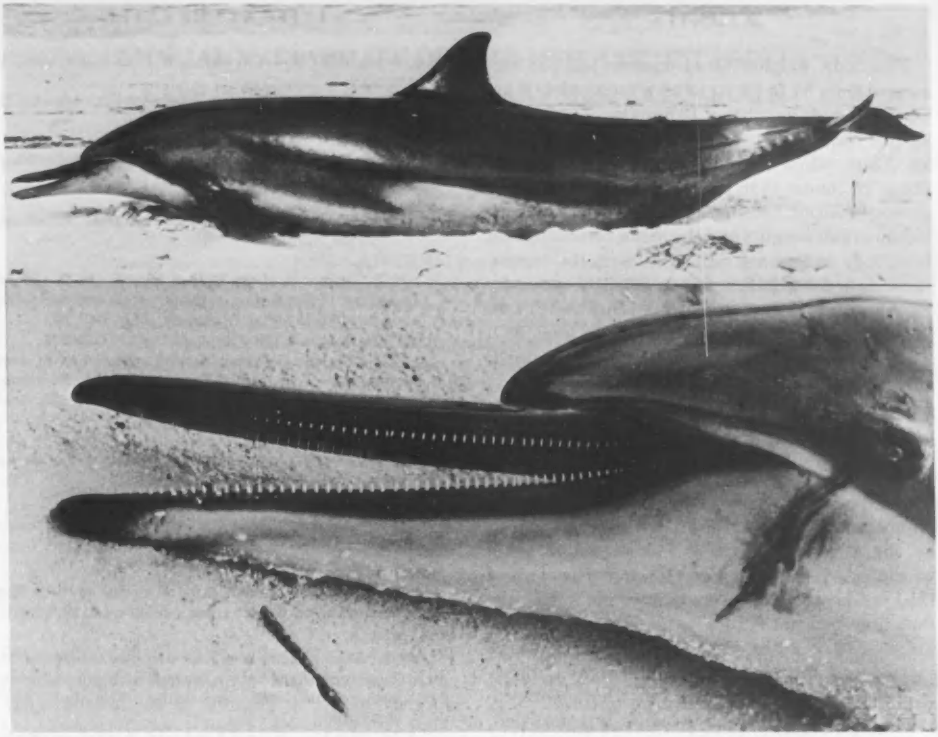

FIGURE 2.—Adult *Stenella longirostris* stranded at Casey Key, Fla. Above adult male, 195 cm total length (504442); below, head of adult female, 186 cm total length (504454).

enough that a larger sample would be needed to demonstrate its validity.

None of the other measurements show any appreciable sexual differences when the differences in total length and rostral length are taken into account.

Since the sample is lacking in intermediate-size animals, there is relatively little that can be said about growth patterns. It is apparent that the snout is relatively shorter and the rest of the head relatively larger in neonatal animals than in adults. The girths appear to be relatively greater, the flippers relatively larger, but the flukes and dorsal fin about the same proportion in the neonates as in the adults. Although the sample of neonates is too small to have any statistical significance, the sexual differences in length of rostrum, position of genital slit, width of flukes, and height of dorsal fin are the same in the neonates as in the adults.

Although comparable data for samples of *S. longirostris* from other areas are sparse (Perrin 1975), this sample appears to be similar to Hawaiian spinners in total length, rostral length, and girths. More meaningful comparison to other populations of *S. longirostris* will require increased sample sizes and more sophisticated statistical procedures.

WEIGHTS

The body weights of 11 males (188-208 cm) ranged from 51 to 75 kg, with a mean of 63.8 kg, while the body weights of 13 females (177-204 cm) ranged from 46.1 to 65.2 kg, with a mean of 55.7 kg. Thus, while the sample of males averaged about 3% longer than the sample of females, they averaged about 14% heavier. The range of individual organ weights and the mean percentages of total body weight are as follows, with the comparable data for Pacific spinner dolphins given by Perrin and Roberts (1972) in parentheses; heart 260-440 g, 0.59% (191-272 g, 0.46%); liver 980-2,200 g, 2.7% (832-997 g, 1.90%); kidneys 350-620 g, 0.78% (289-393 g, 0.65%); brain 500-780 g, 1.02%. The organ weights in the Florida sample, expressed as mean percentage of body weight, averaged about 25% greater than those given for the Pacific spinner dolphins. It is possible that some of this difference is due to weight loss (primarily blubber and muscle) in the Florida sample induced by the stress of whatever factors led to their stranding. As noted earlier, the stomachs of all of the Florida specimens were empty, and it is likely that they had not fed for some time. Perrin and Roberts (1972) noted that in both their samples of spotted and spinner dolphins, the right kidneys tended to be larger than the left whereas in our sample the kidneys were essentially equal (left was heavier in nine, right was heavier in five, and both were equal in eight).

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ANNUAL VARIABILITY OF REEF-FISH ASSEMBLAGES IN KELP FORESTS OFF SANTA BARBARA, CALIFORNIA

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ABSTRACT

Assemblages of kelp-bed fishes that live in and about the kelp canopy or over the reef bottom were censused by movie strips (cinetransects) every September from 1971 to 1974 at rock reefs off Santa Barbara, southern California. Cinetransects provided an adequate and efficient way to estimate species composition (order of relative or ranked species abundances), diversity, and numbers of fish for yearly comparisons between canopy and bottom habitats at mainland and Santa Cruz Island study sites. Canopy assemblages were simpler and more variable than bottom assemblages. They differed less in composition between sites. Between-site differences in fish assemblages reflected differences in structural habitat between mainland and island. Variation in species composition was less among years than between habitats or sites in the sense that site- and habitat-specific composition of assemblages persisted in the course of significant yearly changes in counts of fish and species per transect. Despite these changes, "annual variation," as measured by variance of year-to-year $\log_{10}$ ratios of numbers of 10 common species, was relatively small. Its size was characteristic of stable communities in predictable environments. As a group, planktivores, which form dense aggregations in midwater, fluctuated most in numbers. Perhaps fish responded directly to local changes in water clarity, temperature, currents, and density of giant kelp. However, coincident changes in fish counts at mainland and island sites indicated that these local environmental factors, which did not vary accordingly, were not the only causes of annual variability in fish abundance.

Off southern California, rocky reefs and beds of giant kelp, *Macrocystis pyrifera*, harbor more than 125 species of fish, almost 25% of the Californian marine total (Quast 1968b; Feder et al. 1974). Subtidal reef-fish assemblages have been extensively studied in the warm-temperate San Diegan Faunal Region to the south of Santa Barbara (Quast 1968b, c; Hobson and Chess 1976; Limbaugh[5]), and in the cool-temperate Montereyan Faunal Region to the north (Miller and Geibel 1973; Burge and Schultz[6]; Gotshall et al.[7]). Except for scattered observations and species lists (Hewatt 1946; Quast 1968c; Clarke and Neushul 1967; Neushul et al. 1967; Alevizon 1976), however, virtually nothing is known of the structure and annual variability of such fish assemblages off Santa Barbara, which is at the northern end of the San Diegan Region as defined by Hubbs (1960).

Ebeling et al. (in press) analyzed Santa Barbaran assemblages of kelp-bed fishes sampled from a variety of habitats and localities along the mainland coast and across the Santa Barbara Channel at Santa Cruz Island. The fish community was assumed to comprise smaller groups of species that tend to segregate among habitat types. Photographic observations made throughout 1970 were used to resolve five such "habitat groups." A group of "kelp-rock species" (e.g., garibaldi, *Hypsypops rubicundus*, and California sheephead, *Pimelometopon pulchrum*) was most abundant in relatively clear water and dense kelp over high-relief rocky reef. "Canopy species" (e.g., kelp

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[7]Gotshall, D. W., L. L. Laurent, E. E. Ebert, F. E. Wendell, and G. D. Farrens. 1974. Diablo Canyon power plant site ecological study annual report July 1, 1973—June 30, 1974. *In* W. J. North (editor), Environmental investigations at Diablo Canyon, 1974. Calif. Dep. Fish Game Mar. Resour. Admin. Rep. 74-10, p. 199-305.

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perch, *Brachyistius frenatus*, and señorita, *Oxyjulis californica*) usually aggregated within and just below the kelp canopy; "bottom species" (e.g., gopher rockfish, *Sebastes carnatus*) rested on the rocky reef surface far below; while "commuter species" (e.g., kelp bass, *Paralabrax clathratus*) swam about at all depths. "Inner-marginal species" (e.g., black perch, *Embiotoca jacksoni*) occurred abundantly over mixed rock and sand inshore as well as deeper reefs offshore. Members of different groups tended to mingle in areas of continuous reef and kelp where habitat types were close together. The more complex and extensive island reefs harbored the greatest numbers of "reef specialists" in the kelp-rock group.

The present study is an analysis of annual variability in species composition, diversity, and abundance of kelp-bed fishes in the faunistically transitional (Neushul et al. 1967; Hubbs 1974; Horn and Allen 1978) Santa Barbara Channel. There have been few long-term studies of stability and variability in reef-fish communities (Thomson and Lehner 1976; Sale 1978). Yet, understanding the scope and causes of variation in natural communities has both practical and theoretical importance (Larkin 1978; Wolda 1978). Our primary purposes, therefore, were to 1) document yearly changes in kelp-bed fish assemblages, which had previously impressed us as appearing relatively uniform in time, and 2) relate observed changes to environmental variables that we could readily observe. Secondarily, we assessed the use of underwater movies to census fishes in a complex environment. To these ends, we made annual censuses of fishes in and about the canopy of giant kelp and over the bottom in areas of continuous rock reef at sites off the Santa Barbara mainland and Santa Cruz Island.

METHODS

Study Sites

Sampling was conducted in areas of rocky reef and kelp on either side of the Santa Barbara Channel (Figure 1). Our mainland sampling site was Naples Reef, an isolated system of rocky outcrops and ledges located about 1.6 km offshore, 24

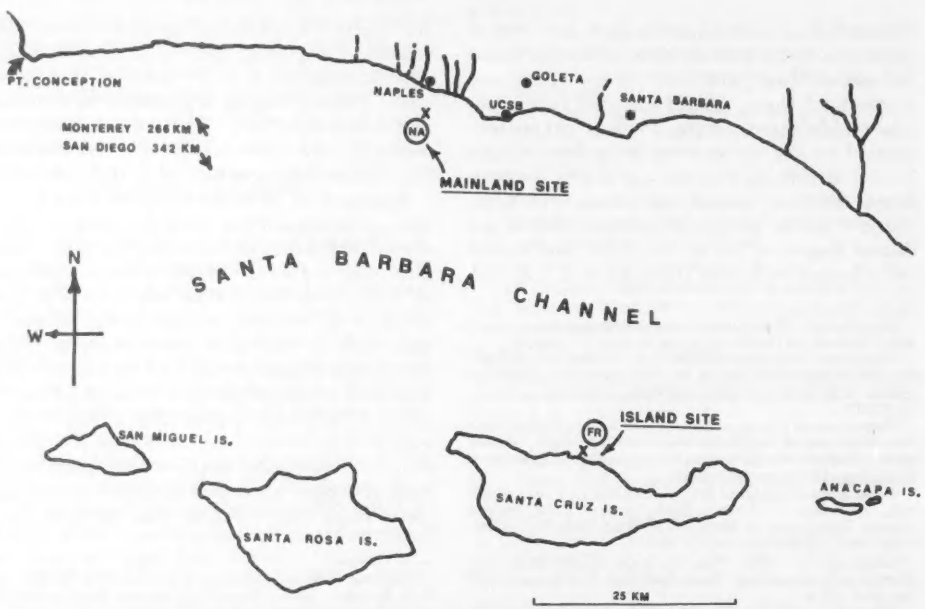

FIGURE 1.—Study sites for yearly sampling of fish assemblages in areas of reef and kelp off Santa Barbara, southern California. Circled letters identify the mainland site, Naples Reef (NA), and the island site, Fry's Harbor and vicinity (FR).

km west of Santa Barbara, Calif. (lat. 34°25′ N, long. 119°57′ W). Measuring 275 × 80 m (2.2 ha), the reef surface averaged 8-12 m in depth, though some crests projected to within 5 m of the surface. The reef was surrounded by flat sand or cobble bottom, 16-20 m deep, with smaller rock outcrops. Above the reef, the kelp canopy usually proliferated during spring and summer, but thinned during late fall and winter.

Island observations were made at a site centered about Fry's Harbor on the north side of Santa Cruz Island (Figure 1). The subtidal substrates here were mostly rocky, with boulder areas, ledges, and caves interspersed occasionally with sand or flat-faced rock. The bottom sloped rather steeply to sand at depths of 15-25 m about 20-50 m from shore. Most sampling was conducted at depths of 3-15 m. Here, the kelp canopy extended a short distance seaward over greater depths and shoreward to meet steep rock cliffs. In contrast with the mainland observations, therefore, most island observations were made within about 10-50 m of the shore, over an area of rapidly increasing bottom depth.

We saw anglers and divers at both sites. Yet, we rarely observed concentrated fishing effort, probably because of the erratic state of the Santa Barbara partyboat industry during the early 1970's (Love and Ebeling 1978). Fishermen in small boats were more frequently seen casting bait and lures near the surface at Naples Reef than at the island site. Hence, catches of kelp bass and other surface predators were probably substantial at Naples Reef only. Sport divers exploited both sites, albeit more sporadically than boat fishermen and seldom during the sampling periods. We suspect that catches of bottom fishes were not large and about the same at both sites.

We noted no kelp cutting and harvesting in the area of either site. About the island site, kelp beds are limited to a narrow band along the steep shore, and so are inaccessible and too small for harvest.[8] Kelp in the mainland area is harvested only inshore of Naples Reef, which is left undisturbed.[9]

Cinetransects

We sampled fish and observed habitat characteristics by means of "cinetransects." These were 2.5-min, Super-8 mm[10] movie films taken at 24 frames/s by scuba divers. The use of 50 ft (15.24 m) film cartridges standardized sampling time, and allowed rapid changing of film. High-speed color film yielded good photographs when water visibility exceeded 3 m. Starting from opportune points within the kelp-rock habitat, divers swam at relatively constant speeds, and, with the camera held level or pointed slightly downward (for bottom transects), steadily panned in about 10° arcs. Large aggregations of fish were photographed in one sweep of the camera; thereafter the camera was not pointed at the aggregation. This procedure allowed rapid and accurate enumeration of aggregations, and avoided redundant sampling of fish. During a given transect, a diver would keep to the same general depth and terrain, so that each transect could be classified by its habitat characteristics. For each transect, he measured depth of filming, depth of bottom, underwater visibility, temperature, and depth of thermocline. Films were taken in two general habitats: bottom and kelp canopy. Canopy transects were made at depths of 2-3 m, just below the mat of floating fronds. Bottom transects were taken from about a meter above the bottom, at depths ranging from about 3 to 15 m. All cinetransects were photographed during September of the years 1971-74. This was in the midst of the season of maximum thermal stratification, when water was predictably calm and clear (Brown 1974; Love and Ebeling 1978).

Two observers counted and tallied individuals per species from cinetransects projected at low speed and stop action. For each film, observers also scored bottom relief and algal density from 1 (low) to 5 (high). They often stopped, reversed, and reran the film to accurately count fish in dense clusters. When observers disagreed, they recounted, and recorded the average of the two closest values. All species but two were tallied separately. The sibling rockfishes *Sebastes carnatus* and *S. chrysomelas*, which were identifiable by color only, were tallied as one, because subtle color differences were not always discernible in cinetransects filmed at greater depths or in more turbid water. Observers did not count small (young-of-year) juveniles, such as the reddish growth stage of blue rockfish, *S. mystinus*. Nor did

[8]Ron H. McPeak, Senior Marine Biologist, Kelco Corp., 2145 East Belt St., San Diego, CA 92113, pers. commun. October 1979.
[9]Bruce W. W. Harger, General Manager, Neushul Mariculture Corp., 275 Orange St., Goleta, CA 93017, pers. commun. October 1979.

[10]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

they count island seaperch, *Cymatogaster gracilis*, in 1971-73 samples. Island seaperch were observed only at Santa Cruz Island, sporadically in dense schools in the kelp canopy. To judge the effect of ignoring this species in 1971-73, we compared two 1974 samples, one with, the other without counts of island seaperch.

Bottom cinetransects were calibrated for area covered by estimating their length and width in the field. We estimated length experimentally by measuring distances swam during transects at Naples Reef. On each of five weekly tests, one diver photographed while a second followed with a tape measure. On 4 of 5 days, one transect went upcurrent, the other downcurrent; on the fifth day, three transects were measured in almost no current. Lengths of all 11 transects averaged 47.8±2.78 m (95% confidence interval—CI). We estimated transect width by counting markers placed along a surveyed course. A tape measure marked the midline of a 50 m stretch of reef flat and rill, and pairs of red floats, anchored 2 m on either side of the tape at 5 m intervals, delimited a 4 m wide band. Four transects were photographed along the course, with divers panning the camera as usual. While viewing the projected films, we estimated widths of pans by taking 4 m (width of the marked band) and adding or subtracting estimated distances before or beyond each float seen at the extremes of the pans. Since widths of 43 pans averaged 4.41±0.288 m (95% CI), the area covered by an average bottom transect was taken as 47.8 m (length) times 4.41 m (width) = 211 m².

Calibration of canopy transects was inherently less accurate. Photographers swam more circuitous routes at more variable speeds in midwater, where light fluctuated between dim and bright. The best we could do was roughly measure distance travelled by a photographer swimming unidirectionally under the canopy: an average length of 62.3 m in four trials both with and against the current. We estimated band width by counting kelp blades (which averaged 0.5 m long) passed during sweeps of the camera: counts usually varied from 8 to 10, translating to 4-5 m. Hence, we assumed band width of canopy transects to equal that for bottom transects (4.41 m), and estimated area covered by a canopy transect as 62.3 m (length) times 4.41 m (width) = 275 m².

Statistical Analyses

Samples were specific for habitat, site, and year. For example, one sample was made up of fish counts from a set of 43 transects filmed in the canopy habitat at the mainland site during 1974.

Sample species diversity of yearly canopy or bottom samples of fish assemblages in mainland and island sites was measured by information-theoretical indices (H), combining species "richness" (total species) and "evenness" (distribution of individuals among species). We used Pielou's (1966) method to estimate population diversity from a set of cinetransects pooled incrementally in random order. Diversity (Brillouin's H) of successively larger subsamples (size k) first increases and then levels off, as the decrease in diversity from adding more individuals of common species balances the increase from adding rare species. Then increments of diversity per added individual (h_k) between adjacent subsample estimates (H_{k-1} and H_k) are independent, and the mean ($\bar{h}$) and variance of h_k's estimate the corresponding population parameters. Species richness (S) was the species count in a whole sample of size $k = n$. Species evenness (J) was the ratio $H_n/\ln S$, where H_n is sample diversity and $\ln S$ (natural log of species count) is the theoretically maximum value of H_n if the S species were equally abundant.

We compared species composition between sites and among years by proportionate similarity and rank correlation. Similarity (I) in species composition was measured as: $I = 1.0 - [0.5(\sum_{i=1}^{S} |p_{ij} - p_{ik}|)]$, where p_{ij} is the proportionate abundance of species i in sample j. Rank correlation (Kendall's tau) was measured between ranked species arrays (Johnson and Koo 1975). Clusters of similar samples were computed from matrices of I by the unweighted pair-group method using arithmetic averages (Sneath and Sokal 1973).

Mean counts of individuals and species per transect were compared between sites and among years (1971-74) by two-way analysis of variance (ANOVA) for unequal and disproportionate subclass sizes, and by one-way ANOVA for unequal sample sizes (Nie et al. 1975; Meeter and Livingston 1978). With variates transformed, sample distributions tended to normality (as indicated by nonsignificant Kolmogorov-Smirnov tests of goodness-of-fit) and sample variances equalized (as indicated by nonsignificant F_{max} tests of largest variance ratios) (Sokal and Rohlf 1969; Meeter and Livingston 1978). A posteriori contrasts among means were obtained by grouping means with nonsignificant ranges (Dunnett 1970; Nie et al. 1975).

Annual variability (AV) in numbers of fish per species was measured as variance in $\log_{10}$ ratios ($\log R$) of estimated numbers per hectare between consecutive years. For each species, we estimated number per hectare by summing mean counts per bottom and canopy cinetransects after correcting canopy means for greater area covered per transect, then multiplying by 47.39, the estimated number of bottom transects covering 1 ha (which approximates the average number per year, 44.12). According to Wolda (1978), $\log R = \log N_i - \log (N_{i-1})$, where N_i is number of individuals for 1 yr and N_{i-1} is that for the preceding year. The mean $\log R$ for an array of species indicates the average net change in species abundance, and the variance of the $\log R$'s (AV) measures the scope of change in species abundances. For example, a mean $\log R$ near zero indicates that about as many species increased as decreased in abundance between years, while a relatively low AV shows that increases and/or decreases were generally small; i.e., that annual variability was low. To increase the reliability of R, only species with at least 5 individuals/ha per year were included in the analysis (Wolda 1978). Although samples covered more than 2 yr, arrays must appear in calculations only once (Wolda 1978). Thus, we computed AV's for an array of 16 $\log R$'s for ratios of species abundances between 1972 and 1971, and for a similar array between 1974 and 1973 (separately for mainland and island study sites). Then, we computed overall AV between the years from the array of 32 $\log R$'s: those for 1972-71 plus those for 1974-73.

RESULTS

Yearly sampling yielded 297 and 331 cinetransects from mainland and island study sites, and recorded 46 fish species in 21 families, although only 31 species in 11 families were common enough to be analyzed (Table 1).[11] On the average, about 35 transects were needed to record 90% of 16 species that were filmed in the kelp-canopy habitat (the "canopy assemblage" of fishes), while 50 transects were needed to record 90% of 31 species that were filmed in the reef-bottom habitat (the "bottom assemblage").

Although our primary objective was to measure yearly variability, our analysis revealed significant differences in species composition, diversity, and abundance of fish assemblages between canopy and bottom habitats, and between mainland and island study sites. Therefore, we describe the observed spatial differences as a prelude to the account of yearly differences.

Spatial Differences

Differences in composition between assemblages in canopy and bottom habitats were obvious and easily demonstrated. For example, canopy and bottom arrays from all years and both sites were segregated in the cluster analysis based on proportionate species abundances (Figure 2). Canopy samples contained relatively more planktivores and kelp browsers like blacksmith, *Chromis punctipinnis*; kelp perch; blue rockfish; juvenile olive rockfish, *S. serranoides*; and señorita (Table 1). Bottom samples contained more bottom grazers and ambushers like pile perch, *Damalichthys vacca*; black perch; garibaldi; California sheephead; gopher rockfish; and black-and-yellow rockfish, *S. chrysomelas*.

The canopy assemblage was simpler than the bottom assemblage in the sense that more individuals of fewer species occurred in the canopy. All of our 31 common species were recorded in bottom cinetransects, but only 16 were filmed in the canopy (Table 1). Furthermore, while the median number of individuals (33—corrected for greater volume per transect) recorded in canopy transects significantly exceeded that (24) for bottom transects, the median species count (5) was significantly less than that (8) in bottom transects (Wilcoxon tests based on 275 canopy and 353 bottom counts, $P<0.005$). These differences were reflected in the shapes of the abundance-diversity curves for the two habitats (Figure 3). Those from the canopy habitats sloped steeply, reflecting the fact that only a few species were relatively common there, while those from the bottom habitats had flatter tops, reflecting a more coequal commonness of several species.

In general, the composition of fish assemblages differed markedly between mainland and island

[11] Additional species that were rarely recorded include: *Heterodontus francisci* (Heterodontidae), *Cephaloscyllium ventriosum* (Scyliorhinidae), *Myliobatis californica* (Myliobatididae), *Torpedo californica* (Torpedinidae), *Syngnathus* spp. (Syngnathidae), *Atherinops affinis* (Atherinidae), *Cymatogaster gracilis* (Embiotocidae—sporadically common at island, see text), *Phanerodon atripes* (Embiotocidae), *Caulolatilus princeps* (Branchiostegidae), *Gibbonsia elegans* (Clinidae), *Coryphopterus nicholsi* (Gobiidae), *Scorpaena guttata* (Scorpaenidae), *Sebastes auriculatus* (Scorpaenidae), *Pleuronichthys coenosus* (Pleuronectidae), and *Mola mola* (Molidae).

TABLE 1.—Relative abundance of 31 species of kelp-bed fishes from canopy and bottom assemblages in yearly cinetransect samples filmed during 1971-74 at mainland and Santa Cruz Island study sites off Santa Barbara, southern California (Figure 1). Values are percent number of individuals.

	Kelp canopy habitat										Reef bottom habitat									
	Santa Barbara mainland					Santa Cruz Island					Santa Barbara mainland					Santa Cruz Island				
Family and species	1971	1972	1973	1974	1971-74	1971	1972	1973	1974	1971-74	1971	1972	1973	1974	1971-74	1971	1972	1973	1974	1971-74
Serranidae:																				
Paralabrax clathratus	9.96	2.87	6.85	2.51	4.56	1.39	3.12	5.47	4.70	3.34	20.78	12.48	6.30	7.01	10.86	9.92	13.39	21.20	10.88	13.82
P. nebulifer	—	—	—	—	—	—	—	—	—	—	0.17	0.05	—	—	0.04	—	—	—	—	—
Sciaenidae:																				
Cheilotrema saturnum	—	—	—	—	—	—	—	—	—	—	—	0.09	0.10	1.45	0.53	—	—	—	—	—
Kyphosidae:																				
Girella nigricans	12.45	—	—	1.11	1.12	1.19	4.21	0.59	3.43	2.72	2.04	10.79	5.92	3.50	7.00	18.39	8.24	10.95	8.46	11.27
Medialuna californiensis	6.51	3.27	1.86	5.09	3.42	0.08	0.26	0.46	0.46	0.28	0.17	0.70	0.67	7.01	2.12	1.13	0.59	0.70	1.40	0.94
Embiotocidae:																				
Brachyistius frenatus	—	—	7.30	0.22	2.28	52.99	37.07	24.70	11.79	34.60	—	—	0.29	0.08	0.08	1.05	1.58	0.16	0.37	0.81
Damalichthys vacca	0.19	0.03	—	0.15	0.06	0.16	0.08	0.13	0.06	0.10	9.03	4.77	6.69	4.70	5.66	2.58	4.22	4.12	2.87	3.48
Embiotoca jacksoni	—	0.07	—	0.44	0.11	—	—	0.13	0.58	0.13	23.34	22.62	43.55	25.90	27.91	8.63	7.92	7.22	6.84	7.64
E. lateralis	—	0.23	—	0.66	0.22	0.04	0.31	2.50	0.70	0.66	2.56	6.45	3.92	1.88	4.37	2.18	3.10	4.35	1.84	2.87
Hypsurus caryi	—	—	—	—	—	—	—	—	—	—	2.39	2.94	7.74	17.95	7.65	—	0.46	0.08	—	0.15
Phanerodon furcatus	2.68	—	2.81	0.44	1.15	—	—	0.33	0.58	0.16	0.17	0.75	2.20	0.51	0.93	0.32	0.59	0.31	0.81	0.52
Rhacochilus toxotes	0.19	—	0.04	—	0.03	0.04	—	—	—	0.01	5.96	1.92	1.62	0.77	2.04	0.16	1.91	1.24	1.18	1.17
Pomacentridae:																				
Chromis punctipinnis	51.92	29.00	37.48	42.03	35.79	39.72	35.46	11.13	39.95	33.49	9.03	7.71	2.20	10.68	7.44	16.69	7.26	0.54	25.88	12.51
Hypsypops rubicundus	—	—	—	—	—	—	—	—	—	—	—	1.26	0.76	1.45	1.05	13.14	17.08	10.87	12.35	13.51
Labridae:																				
Halichoeres semicinctus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.32	0.33	0.16	0.29	0.28
Oxyjulis californica	4.60	3.76	15.02	10.03	8.51	1.11	3.98	8.96	11.61	5.42	8.52	8.97	2.67	5.47	6.76	1.69	2.38	3.18	5.81	3.28
Pimelometopon pulchrum	—	0.03	0.04	—	0.03	—	0.05	—	0.06	0.03	2.22	4.16	2.10	1.11	2.77	13.39	11.68	9.86	8.31	10.79
Clinidae:																				
Heterostichus rostratus	0.19	0.07	0.27	0.30	0.18	0.08	0.03	0.07	—	0.04	—	0.09	0.76	0.94	0.42	—	0.13	—	0.15	0.07
Scorpaenidae:																				
Sebastes atrovirens	0.38	0.30	0.50	0.22	0.35	1.39	2.62	3.49	8.30	3.47	0.51	0.28	0.67	0.59	0.47	6.05	8.31	7.38	5.52	6.88
S. carnatus & S. chrysomelas	—	—	—	—	—	—	—	—	—	—	2.22	0.75	3.25	2.39	2.00	0.56	2.31	2.48	0.88	1.59
S. melanops	—	—	—	—	—	—	—	—	—	—	—	—	0.19	—	0.04	—	—	—	—	—
S. mystinus	10.92	59.81	27.49	35.18	41.26	0.04	10.63	3.82	9.76	6.67	7.16	11.03	4.20	2.74	7.12	0.56	5.08	11.57	3.68	5.24
S. rastrelliger	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.56	0.53	0.47	0.22	0.44
S. serranoides	—	0.56	0.36	1.62	1.67	1.72	2.18	38.21	8.01	8.85	1.02	0.28	0.10	0.68	0.42	1.05	1.38	1.94	1.47	1.46
S. serriceps	—	—	—	—	—	—	—	—	—	—	0.17	—	0.10	—	0.04	0.16	0.20	0.08	0.22	0.18
S. vexillaris	—	—	—	—	—	—	—	—	—	—	0.17	0.09	—	—	0.06	—	—	0.08	—	0.02
Hexagrammidae:																				
Ophiodon elongatus	—	—	—	—	—	—	—	—	—	—	—	0.05	0.38	—	0.10	—	—	—	—	—
Oxylebius pictus	—	—	—	—	—	—	—	—	—	—	2.39	1.68	3.25	2.91	2.39	1.45	1.12	0.85	0.59	1.00
Cottidae:																				
Leiocottus hirundo	—	—	—	—	—	—	—	—	—	—	—	—	0.10	—	0.02	—	—	0.08	—	0.02
Scorpaenichthys marmoratus	—	—	—	—	—	—	—	—	—	—	—	0.05	0.29	0.26	0.14	—	0.20	0.16	—	0.09
Number of individuals	522	3,031	2,204	1,356	7,113	2,442	3,847	1,518	1,722	9,529	587	2,140	1,047	1,170	4,944	1,240	1,516	1,288	1,360	5,404
Number of cinetransects	13	31	45	40	129	22	38	46	40	146	25	45	55	43	168	37	45	55	48	185

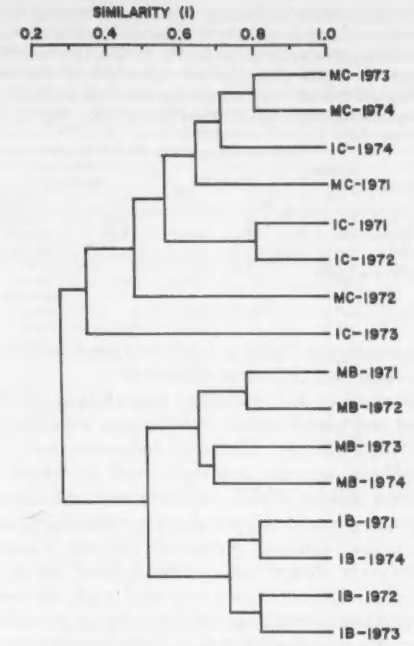

FIGURE 2.—Clustering, by year (right number), of canopy (C) and bottom (B) cinetransect samples of kelp-bed fishes filmed each September in 1971-74 at mainland (M) and Santa Cruz Island (I) study sites off Santa Barbara, southern California.

study sites. Samples from within mainland or island sites tended to be more alike than samples between these sites, particularly for bottom assemblages. Samples from within tended to form secondary subclusters nested in the principal ones distinguishing canopy and bottom assemblages (Figure 2), and within-site similarity values tended to be higher than between-site values (Table 2).

As indicated by clusters (Figure 2) and similarity values (Table 2), however, mainland and island canopy assemblages were more difficult to distinguish than bottom assemblages. The mean ratio of within- to between-site resemblance (I or tau) was comparatively large for arrays of canopy species (Table 2), indicating that canopy assemblages were only slightly more distinguishable between sites than among years. This, and the fact that variances of canopy similarities were relatively large (Table 2), explained why the clusters of canopy samples were poorly defined. What few between-site differences in canopy samples prevailed were due to greater numbers of kelp perch and juvenile olive rockfish observed in the canopy habitat of the island site, and of blue rockfish at the mainland (Table 1). Island canopy samples contained a few more species than mainland canopy samples (Table 3, S), and the average number of species per cinetransect (Table 3) was significantly greater (Table 4) at the island. (The significant year-site interaction as indicated in

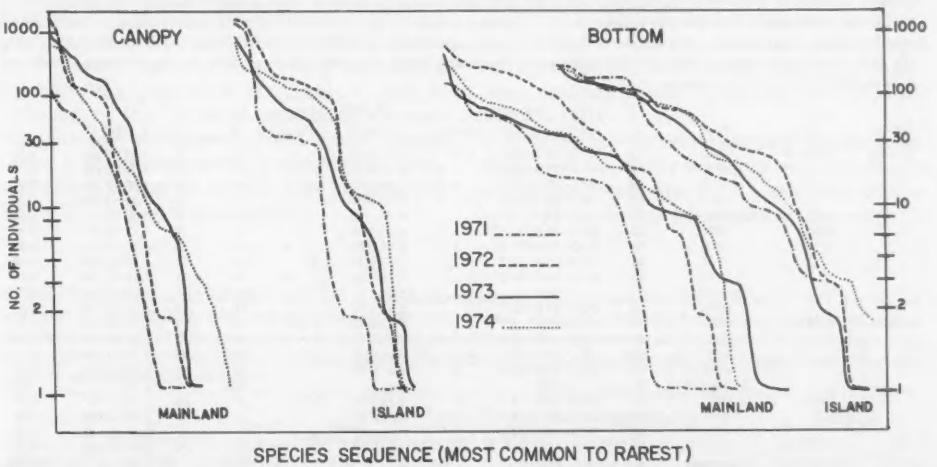

FIGURE 3.—Abundance-diversity curves for 31 species of kelp-bed fishes from canopy and bottom assemblages in yearly samples filmed during 1971-74 at mainland and Santa Cruz Island sites off Santa Barbara, southern California.

TABLE 2.—Comparison of within-site and between-site means (±1 standard deviation) of similarity (I) and rank correlation (tau) between all pairs of species-abundance arrays from yearly cinetransect samples filmed during 1971-74 at mainland and Santa Cruz Island Study sites off Santa Barbara, southern California. Within-site means are of values for all pairs (1971 vs. 1972, 1971 vs. 1973, . . ., 1973 vs. 1974), both members of which were filmed in canopy or bottom habitats either at the mainland or island site; between-site means are of values for all such habitat-year pairs, one member of which was from an island sample, the other from a mainland sample; and mean ratio is the between-site value/mean within-site value (mainland and island). (Figure 2 is a cluster diagram of yearly samples, computed from all values of I.)

	Within sites (n = 6)[1]				Between sites (n = 10)		Mean ratio between/within	
	Mainland		Island					
Habitat	I	Tau	I	Tau	I	Tau	I	Tau
Canopy	0.62±0.11	0.58±0.09*	0.61±0.13	0.59±0.09*	0.50±0.17	0.45±0.12	0.81	0.77
Bottom	0.68±0.05**	0.67±0.06***	0.75±0.06***	0.80±0.03***	0.53±0.09	0.49±0.06	0.74	0.67
Mean	0.65	0.625	0.68	0.695	0.515	0.495	0.775	0.72

[1]Difference of within- and between-site means significant at (t-test): *P < 0.05; **P < 0.01; ***P < 0.001.

Table 4 occurred because the relation was reversed in 1973 as indicated in Table 3.) Diversity and evenness (Table 3, $\bar{h}$ and J) of canopy assemblages, however, did not differ significantly between sites.

However, sporadically abundant endemic island seaperch were not included in these comparisons. Adding this species to 1974 counts of the island-canopy samples increased the fish total from 1,722 to 3,084 individuals, median fish counts per transect from 31 to 64 individuals, and median number of species per transect from 5.5 to 6.0. The slight increase in species diversity ($\bar{h}$) was not significant (Table 3). Island seaperch were seldom observed in bottom transects.

In contrast to the canopy assemblages, mainland and island bottom assemblages were easily distinguishable. Because between-site resemblance was comparatively small for arrays of bottom species (Table 2), mainland and island clusters of samples were sharply defined (Figure 2). Island samples contained relatively more California sheephead, garibaldi, and opaleye, *Girella nigricans*, and included rock wrasse, *Halichoeres semicinctus*, which were not recorded from the mainland (Table 1). Mainland-site sam-

TABLE 3.—Yearly abundance and species diversity of canopy and bottom assemblages of kelp-bed fishes in cinetransect samples from mainland and Santa Cruz Island study sites off Santa Barbara, southern California. Columns include: n, no. of transects in sample; Geom. $\bar{x}$, the antilog of the mean transformed fish count with 95% confidence limits; S, total species in sample; $n(\bar{h})$, sample size to compute $\bar{h}$; $\bar{h}$, the mean of successively pooled transect estimates of diversity per individual (see text); and J, evenness of distribution of individuals among species in the sample. Contrasts among means that were shown to differ significantly by analysis of variance (Table 4) were by the Student-Newman-Keuls procedure (Sokal and Rohlf 1969:239); means making up homogeneous subsets are indicated by X's in the same column.

				Fish counts		Species counts					
Habitat	Site	Year	n	Geom. $\bar{x}$, 95% CL	Contrasts	$\bar{x}$ ±95% CI	Contrasts	S	$n(\bar{h})$	$\bar{h}$ ±95% CI	J
Canopy	Mainland	1971	13	11.0<24.2<53.1	x x	2.7±0.63	x	11	7	1.33±0.555	0.54
		1972	31	47.4<70.6<105.0	x	4.7±0.57	x	12	19	1.32±0.297	0.39
		1973	45	32.2<39.9<49.3	x	5.0±0.42	x	12	27	1.80±0.161	0.64
		1974	40	16.2<22.5<31.2	x	4.3±0.57	x	14	29	1.82±0.216	0.52
		Unweighted	$\bar{x}$	39.3		4.2		12.2		1.57	0.522
	Island	1971	22	30.6<58.8<112.5	x	4.6±0.69	x	13	16	1.17±0.187	0.40
		1972	38	51.0<70.6<97.9	x	6.2±0.67	x	13	29	1.63±0.137	0.61
		1973	46	19.6<25.4<32.6	x	3.5±0.45	x	14	32	1.70±0.301	0.58
		1974	40	21.5<29.0<39.3	x	5.7±0.63	x	14	27	2.18±0.199	0.71
		Unweighted	$\bar{x}$	46.0		5.0		13.5		1.67	0.575
		1974[1]	40	30.3<43.9<63.7		6.3±0.71		15	29	2.32±0.272	0.64
Bottom	Mainland	1971	25	15.7<20.0<25.4	x x	7.3±0.82	x x	20	11	2.39±0.167	0.75
		1972	45	36.6<42.4<48.9	x	10.1±0.62	x	24	27	2.51±0.130	0.76
		1973	55	13.7<16.2<19.3	x	7.0±0.65	x	25	31	2.34±0.185	0.68
		1974	43	18.9<22.8<27.4	x	8.2±0.83	x	22	33	2.46±0.116	0.77
		Unweighted	$\bar{x}$	25.4		8.2		23.0		[2]2.42	0.740
	Island	1971	37	23.6<28.6<34.6	x	8.7±0.65	x x	21	25	2.45±0.107	0.77
		1972	45	24.1<28.7<34.2	x	9.5±0.84	x	24	36	2.60±0.089	0.82
		1973	55	16.9<19.9<23.5	x	7.8±0.72	x	25	34	2.56±0.123	0.78
		1974	48	17.0<21.3<26.7	x x	7.6±0.66	x	22	28	2.69±0.169	0.77
		Unweighted	$\bar{x}$	24.6		8.4		23.0		[2]2.58	0.785
		1974[1]	48	17.9<22.0<29.2		7.8±0.67		23	30	2.83±0.179	0.79

[1]Including counts of *Cymatogaster gracilis*.
[2]Difference between unweighted means of mainland and island values significant at P = 0.05.

TABLE 4.—Analysis of variance of kelp-bed fish counts (log_{10} transformed) and species counts from cinetransects composing yearly samples filmed during 1971-74 in canopy and bottom habitats. For the two-way ANOVA's, samples were classified by sites (Santa Barbara mainland and Santa Cruz Island, southern California) and years (four sequential Septembers). For the one-way ANOVA's, samples were classified by years for each site separately (Mainland and Island subheads).

Source	df	Fish counts MS	Fish counts F	Species counts MS	Species counts F
Canopy:					
Sites, S	1	0.062	<1	17.631	6.17**
Years, Y	3	2.802	16.78***	32.629	11.42***
SY	3	1.079	6.46***	46.414	16.24***
Error	267	0.167		2.858	
Mainland:					
Years	3	1.598	8.93***	19.744	8.37***
Error	125	0.179		2.360	
Island:					
Years	3	2.282	14.56***	59.298	17.99***
Error	142	0.157		3.296	
Bottom:					
Sites, S	1	0.001	<1	2.777	<1
Years, Y	3	1.408	19.51***	106.177	18.07***
SY	3	0.420	5.83***	19.187	3.26*
Error	345	0.072		5.877	
Mainland:					
Years	3	1.505	23.48***	88.720	15.99***
Error	164	0.064		5.547	
Island:					
Years	3	0.322	4.05**	36.639	5.93***
Error	181	0.080		6.176	

*$P \approx 0.02$; **$P \approx 0.01$; ***$P < 0.001$.

ples, on the other hand, included relatively more black perch, pile perch, and rainbow seaperch, *Hypsurus caryi*. Whereas one species—the black perch—usually dominated mainland samples, several species—the kelp bass; opaleye; blacksmith; garibaldi; and California sheephead—were often equally abundant in island samples. This more equitable spread of numbers over several common species resulted in significantly greater species diversity ($\bar{h}$) by increasing the evenness component (J) (Table 3), and is reflected in the flattened tops of dominance-diversity curves (Figure 3). Neither total species (Table 3, S) nor mean number of species per transect (Table 3, species counts) were significantly larger (Table 4) in island samples.

Mainland and island study sites differed significantly in certain characteristics of structural habitat (Table 5). Scored relief of reef bottom was significantly greater at the island site, although scored densities of giant kelp and bottom algae did not differ significantly between sites. Even though depth of reef over which bottom transects were filmed did not differ significantly between sites, it was more variable at the island site (Table 5) because the shore there sloped more steeply (Figure 4). Discounting 1973, when water at the island site was unusually turbid, underwater visibility was significantly greater by some 2.0 m at the island site (Table 6). Island water temperatures were significantly greater, though only slightly so, in all yearly sampling periods except 1973.

Yearly Differences

Species composition of bottom assemblages at mainland and island sites was more uniform (showed greater resemblance among years) than the corresponding canopy assemblages (Table 2), although significantly so only for the island site (t-tests, I between habitats, $P<0.05$; tau, $P<0.002$). Consequently, both measures of yearly resemblance (I, tau) of bottom-species arrays within sites were significantly greater than those between sites (Table 2). Furthermore, among-year variances of both resemblance measures for mainland- and island-bottom assemblages were less than those for both canopy assemblages, though significantly so only for island measure tau (F-test, $P \approx 0.05$). Comparing bottom assemblages only, the island assemblage was significantly more uniform (t-tests, I between sites, $P \approx 0.05$; tau, $P<0.001$).

Fish and species counts also reflected the greater annual variability of canopy assemblages. We computed coefficients of variation (CV)—percentage ratios of standard deviation to

TABLE 5.—Means of habitat variables measured with each cinetransect for all bottom samples filmed during 1971-74 at mainland and Santa Cruz Island study sites off Santa Barbara, southern California. Scored from 1 (low) to 5 (high), plant density, other algae includes all understory forms. Time of day is the 4-yr range of median times at which transects making up yearly samples were filmed. CV is coefficient of variation and CI, confidence interval. Significance levels are from Mann-Whitney U-tests of rank differences between mainland and island values.

Site	No. of observations (n)	Time of day (h)	Mean bottom type score	Mean plant density score: Giant kelp	Mean plant density score: Other algae	Bottom depth (m): $\bar{x}$ ±95% CI	Bottom depth (m): CV	Underwater visibility (m): $\bar{x}$ ±95% CI	Underwater visibility (m): CV
Mainland	168	1205-1403	3.89	2.43	3.16	8.62±0.205	15.4%	6.11±0.157	17.4%
Island	185	1210-1400	4.43**	2.29	3.29	8.28±0.400	32.8%	[1]8.11±0.439	[1]34.8%

**$P<0.01$.
[1] n = 130, excluding unusually low values for 1973 (see Table 6).

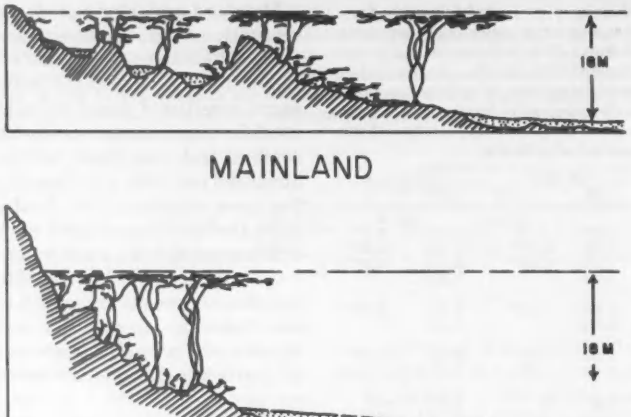

FIGURE 4.—Offshore profiles (vertically exaggerated) at mainland (Naples Reef) and Santa Cruz Island (Fry's Harbor) study sites off Santa Barbara, southern California. Off the mainland, broad sand and cobble flats (stippled) separate rocky outcrops (hatched) between the shore and Naples Reef (highest outcrop), 1.6 km offshore. Off the island, the relatively steep rocky bottom meets sand within only about 50 m of shore.

TABLE 6.—Yearly means (±95% confidence interval) of diver estimated underwater visibility and temperature measured with each cinetransect in bottom-habitat samples filmed during 1971-74 at mainland and Santa Cruz Island study sites off Santa Barbara, southern California.

Site	Year	n	Underwater visibility (m)	Water temperature, surface (°C)	Thermocline depth (m)
Mainland	1971	25	5.61±0.436	16.51±0.309	8.90±0.704
	1972	45	7.07±0.222	18.00±0.081	8.72±0.219
	1973	55	6.43±0.317	17.31±0.060	8.72±0.326
	1974	43	4.97±0.347	19.16±0.076	8.78±1.036
Island	1971	37	7.96±0.363	19.42±0.063	10.00±0.329
	1972	45	8.84±0.991	18.56±0.335	10.45±0.951
	1973	55	2.97±0.082	16.63±0.250	Undetected
	1974	48	7.56±1.070	19.56±0.070	>10-11

mean—to compare variability of these different measures of different magnitudes (Sokal and Rohlf 1969:62). Averaged among eight yearly samples (four mainland + four island, summarized in Table 3), CV's for counts per transect of individuals and species in canopy samples ($\bar{x}$ = 75.5% and 36.9%) were significantly greater than corresponding values (61.1%, 29.0%) for bottom samples (t-tests, $P<0.05$). Expectedly, therefore, the CV for species diversity ($\bar{h}$) of canopy samples was also significantly greater ($\bar{x}$ = 33.8% vs. 13.6%, approximate t-test, unequal variances, $P<0.05$).

Yearly differences in mean fish and species counts per transect (canopy and bottom) were highly significant (Table 4). All one-way ANOVA's revealed such differences (Table 4), and highs and lows generally coincided between mainland and island sites (Table 3). For example, counts were generally high in 1972, low in 1973, and intermediate in 1971 and 1974. Thus, most of the significant differences between means were due to a relatively abrupt decline from high counts in 1972 to low counts in 1973. The 1972 peak was most pronounced at the mainland site, when 10 of 16 species had greatest abundances, vs. 7 at the island (Table 7). Peaks of five species coincided: *Paralabrax clathratus*, *D. vacca*, *E. lateralis*, *S. atrovirens*, and *S. mystinus*. The only other coincident peak abundance was of *S. serranoides* in 1973. Despite the general correspondence between sites of overall changes in abundance and species number, however, significant year-site interactions (Table 4) indicated notable exceptions. For example, 1973 counts of individuals and species were relatively high in the mainland canopy, but low in the island canopy (Table 3).

Wolda's (1978) measures of annual variation revealed overall trends in species abundances

TABLE 7.—Annual variation of estimated density (individuals per hectare) of common kelp-bed fish species at mainland and Santa Cruz Island study sites off Santa Barbara, southern California. Variance $\sqrt{n}$, the variance of square roots of yearly densities, measures yearly variability discounting effects of means; $\bar{R}$ at bottom of table, the mean of log R's—the average difference in $\log_{10}$ density for the species array between two successive years, measures net change in the array; AV, the variance of log R's, measures the scope of change. Between-year totals yield these statistics for an array of all 12 log R's (See text and Wolda 1978). A dash (—) indicates that the number was too small for analysis.

	Mainland					Island				
Species	1971	1972	1973	1974	Variance $\sqrt{n}$	1971	1972	1973	1974	Variance $\sqrt{n}$
Paralabrax clathratus	377	384	171	121	19.3	214	329	301	220	3.1
Girella nigricans	204	246	53	59	19.2	340	272	128	167	10.6
Medialuna californiensis	97	132	39	153	8.1	21	19	13	26	0.4
Brachyistius frenatus	—	—	—	—	—	2,161	1,394	299	190	247.9
Damalichthys vacca	103	109	60	62	2.1	47	70	47	39	0.8
Embiotoca jacksoni	260	512	383	339	7.3	137	117	82	101	1.3
E. lateralis	28	154	35	32	11.6	37	61	48	36	0.7
Hypsurus caryi	27	66	70	231	18.0	—	—	—	—	—
Rhacochilus toxotes	67	43	15	10	5.5	5	30	14	16	1.8
Chromis punctipinnis	864	1,207	689	657	17.4	1,872	1,420	140	976	187.5
Hypsypops rubicundus	—	—	—	—	—	208	273	108	167	6.6
Oxyjulis californica	161	336	280	194	6.6	71	185	143	260	10.4
Pimelometopon pulchrum	25	95	20	14	7.4	213	189	109	113	4.5
Sebastes atrovirens	11	74	15	10	6.7	154	229	124	204	3.3
S. carnatus & *S. chrysomelas*	25	17	29	31	0.4	10	23	19	12	0.6
S. mystinus	238	2,379	531	470	217.3	11	472	175	203	57.2
S. serranoides	11	26	66	29	3.9	85	102	481	145	34.3
Oxylebius pictus	27	38	29	38	0.3	—	—	—	—	—
$\bar{R}$ Between years		0.29	−0.30	0.00			0.23	−0.24	0.06	
Between-year total			0.15					0.14		
AV Between years		0.12	0.12	0.06			0.20	0.12	0.09	
Between-year total			0.11					0.15		
Mean variance, midwater planktivores					117.3					164.2
Mean variance, all others					8.3					6.0

(Table 7). In general, mean log R's (Table 7, $\bar{R}$), which measure net annual change between species arrays, differed significantly within (t-tests, $P<0.01$), but not between ($P>0.05$) sites. This further indicated that species abundances varied concordantly on both sides of the Channel. For the mainland site, $\bar{R}$ for 1971-72 was positive, indicating net increases in most species between these years (Table 7) as total fish counts increased significantly both in canopy and bottom habitats (Table 3); was negative for 1972-73 as numbers decreased in both habitats; and was zero for 1973-74 as a decrease in total canopy numbers offset an increase in bottom numbers. Net annual changes at the island site were somewhat less marked (Table 7), and numbers of fish differed significantly between 1972 and 1973 only (Table 3). In general, variances of log R's (Table 7, AV), which measure the scope of annual differences between species arrays, did not differ significantly either within or between sites (F-tests, $P>0.1$). However, the within-site differences were more marked, which is consistent with the concordance of annual trends of the mainland and island sites.

Much of the yearly variation in fish abundance was due to fluctuations in species that aggregate in the kelp canopy, especially midwater planktivores (Table 7). The average among-year variance of transformed numbers of three abundant planktivores (*B. frenatus*, *Chromis punctipinnis*, and *S. mystinus*) was relatively large (145.4, $n = 5$); that for abundant species whose vertical distributions are somewhat broader (*Paralabrax clathratus*, *G. nigricans*, *S. serranoides*, and *O. californica*) was substantially less (13.4, $n = 8$); while that for abundant demersal species (*E. jacksoni*, *Hypsypops rubicundus*, and *Pimelometopon pulchrum*) was smaller still (5.4, $n = 5$).

Yearly differences were loosely related to underwater visibility, water temperature, and, perhaps, to kelp density in the canopy. Water was relatively clear and warm during September 1972 (Table 6) when counts of individuals and of species were high. Furthermore, water was turbid and cool at the island site during 1973 when counts were low. However, at the mainland site in 1973, where no such conditions prevailed (Table 6), bottom counts were also low (Table 3). Kelp density seemed to affect canopy counts at the mainland site, where lower scores for kelp density in 1974 (Table 5) coincided with lower counts of fish in the canopy (Table 3).

In sum, variation in composition (order of relative or ranked species abundances) was less

between years than between habitats or sites, although canopy assemblages maintained less site-specific integrity than bottom assemblages. Coincident peak abundances of several species at both sites in 1972 contributed to significant yearly differences in fish counts, although significant year-site interactions revealed exceptions to the generally concordant annual trends. Fishes that aggregated in the canopy habitat, especially midwater planktivores, probably contributed most to annual variation measured by between-year log ratios of numbers per species. Yearly differences in fish abundances were loosely related to water clarity and temperature and kelp density, but correlations were not clear-cut.

DISCUSSION

Sampling

With limited time, personnel, and budget, visual transecting may be the most appropriate method for sampling fish populations in the complex reef environment, so long as it is understood that this method always underestimates densities of small, hidden, and/or cryptic species (Brock 1954; Jones and Chase 1975). Although some investigators aver that destructive methods (poisoning, dynamiting) provide broader sampling (Randall 1963; Goldman and Talbot 1976), others counter that visual methods are more representative because they record individuals of larger, stronger species that escape the slaughter (Smith and Tyler 1973). Hence, a thorough census of covert and overt species probably requires both methods (Quast 1968c).

Cinetransecting is analogous to visual transecting. Both methods may miss most covert fish (Alevizon and Brooks 1975), but record most overt individuals. For example, the rank order of species abundances from all mainland-bottom samples (Table 1) correlated significantly (tau = 0.66, $P<0.001$) with that of daytime visual transects made along a transect line about the reef crest at this site throughout the year (Ebeling and Bray 1976: table 3). Four of the five top-ranking species were the same in both studies, even though cinetransects covered a much broader area.

However, cinetransects have some advantages over visual transects. They can be made quickly, as many as 50/d in the present study. Cinetransects provide permanent records of the fish and their environment, not only for greater accuracy in identifying and counting fish, but also for reuse in related studies (see Alevizon 1975; Bray and Ebeling 1975; Love and Ebeling 1978). Diver photographers can proceed slowly and steadily, not diverting their attention from sampling to record observations or follow a transect line. They do not need extensive training in quick recognition of fish species and numbers, so can be replaced by others if required; if cinetransect samples are sorted into subsets, each filmed by one or the other of two different divers, correlations between the corresponding diver-specific species arrays are very high. For example, the four habitat-site-specific samples filmed by two divers in 1973, when sorted to eight diver-specific subsets, gave tau rank correlations ranging from 0.71 to 0.89 ($P<0.001$).

Within broad limits, furthermore, water visibility and light levels probably do not appreciably affect the volume of water sampled by cinetransects filmed along the bottom. At a given focus distance, the camera lens' depth of field is inversely related to the diameter of its aperture. In bright light, the aperature is small, creating a greater zone in which objects are in focus. In the kelp forest, however, light was generally so dim, even on clear days, that the aperture was almost always fully open. Thus, shading probably creates a fairly constant depth of field. To check this, we estimated the distance at which objects were first identifiable on film. Two divers swam along a tape measure ending in a fishlike target, one filming the target and nearby fish, the other signaling distance from target. During the first trial when underwater visibility (distance at which target was discernible) was 15.2 m, fish were identifiable on film only when photographed within about 3.5 m of the camera. During the second when visibility was only about 4.0 m, fish were still identifiable when photographed within about 3 m. Hence, the fairly constant depth of focus of the camera's lens, which was always set at 2.0 m on the distance scale, standardized the maximum distance (about 3.5 m) at which a photographed fish was identifiable.

Linear regressions of $\log_{10}$-transformed fish counts on estimated underwater visibility provide further evidence that visibility had little effect on values. Mean fish and species counts for the 1973 and 1974 island-bottom samples were similar, so the two were combined as one large sample (n = 103) for regression analysis. Although visibility varied between 2.1 and 15.2 m, the regression was nonsignificant (ANOVA F-test, P = 0.3). Even in

the canopy habitat, the effect of more variable light levels is apparently not severe. A similar regression analysis of pooled 1971-72 island-canopy samples ($n = 60$) was nonsignificant ($P = 0.9$), though visibility ranged from 4.6 to 10.7 m.

But while such inferences from camera optics and counts-visibility relations indicate that estimates of relative abundance obtained from cinetransects are comparable over a wide range of sampling conditions, we feel that the calibration of absolute densities presents difficulties. The primary problem is that, particularly in the kelp canopy, our estimates of area or volume sampled are tenuous. For this reason, we used absolute densities only for computing Wolda's (1978) measure of annual variation, which required estimated abundances per species, standardized for differences in sampling effort among years and between canopy and bottom habitats. We feel that this is proper because a systematic error in estimating will have little effect on the measure's value, which is based on yearly ratios of population sizes, not on sizes per se.

Also, combining canopy and bottom transects may miss some fish at middepth. Canopy transects covered depths between 1 and 4 m, which included the greatest concentration of fish in the upper water column. Bottom transects covered depths between the reef and about 2 m upward, which included greatest concentrations in the lower column. Nonetheless, over bottoms averaging 8.5 m deep, cinetransects generally missed the top meter as well as midwater between 4 and 6.5 m. Hence, our fish counts, even of overt midwater species, probably underestimated true abundances.

Annual Variability

Species composition (order of relative or ranked species abundances), rather than richness (number of species), contributed most to differences between mainland and island fish assemblages, which were most marked for the bottom assemblages (see also Ebeling et al. in press). Yearly mainland and island samples had the same number of species, although island species diversity was slightly greater because individuals were more evenly distributed among species. At the island site, species in a "kelp-rock" habitat group (Ebeling et al. in press)—tropically derived species such as *Pimelometopon pulchrum* and *G. nigricans*—were relatively more abundant than at Naples Reef. We had no indication that fishing intensity for such species (spear fishing, bottom angling) differed between the two sites. Nor was unnatural disturbance by kelp harvesting a factor. Furthermore, virtually unexploited kelp-rock species, such as *Hypsypops rubicundus*, were relatively more abundant at Santa Cruz Island. This indicates that much of the mainland-island difference in species composition probably reflected the observed differences in structure of natural habitat rather than differences in exploitation. Likewise, but on a broader scale, insular and continental shore-fish faunas are distinguished in the tropical western North Atlantic (Robins 1971; Gilbert 1972). Whereas turbid waters, muddy-silty bottoms, and few reefs characterize mainland habitats, clear water, coral reefs, and more stable conditions typify island habitats. Consequently, island fish assemblages contain relatively more specialized reef species, such as pomacentrids and labrids, that require the trappings and provisions of complex surfaces.

We felt that composition and abundance of the fish assemblages remained fairly constant among years, considering that they inhabit a presumed zone of faunal transition (Hubbs 1974; Horn and Allen 1978). Species composition varied more between sites and habitats than among years. This indicates that a particular assemblage persists, despite significant yearly variation in its fish and species counts. Yet we had few standards for comparison. Sale (1978:85) knew of no evidence that demonstrated "long-term local stability in reef fish communities," presumably because long-term monitoring studies were wanting. With a 7-yr study of fishes inhabiting a rocky tidal pool in the northern Gulf of California, however, Thomson and Lehner (1976) showed that fish abundance, diversity, and species order were seasonally predictable and varied little from year to year. In fact, the fish assemblage was remarkably resilient, recovering quickly from unpredictable and devastating disturbances, such as severe storms, winter kills, and rotenone poisoning. More generally, Wolda (1978) emphasized the need for actual measures of annual variability in tropical and other animal assemblages to test a plethora of theoretical speculation.

Our values of Wolda's (1978) measure of annual variation (AV) in arrays of species were in fact relatively low. AV's for fish assemblages at mainland and island sites (0.11, 0.15) did not differ significantly (F-tests of variance ratios) from most of those (0.06-0.33, averaging 0.15) for arthropods

living in humid, climatically stable and more predictable areas, but were significantly less than most values (0.12-0.64, averaging 0.34) for arthropods living in dry, climatically unstable environments (Wolda 1978: table 2). Values of AV (0.17, 0.20) that we calculated from annual sight transects of reef fishes taken off central California by Miller and Geibel (1973) and Burge and Schultz (see footnote 6) exceeded our values, but not significantly so. But our AV's were significantly less than the value (0.55) that we calculated from Livingston's (1976) trawl samples of fish from a Florida estuary during two successive winters (*F*-tests of variance ratios, $P<0.01$). Thus, annual variation in species abundances of our fish assemblages may be more typical of communities in relatively stable environments than of those from highly variable environments.

Climatic and other environmental anomalies may contribute to annual variation. Peak fish abundance in 1972 occurred in relatively clear and warm water, which may stimulate fish to be more active (Quast 1968a, b, c; Larson 1977), and perhaps more easily photographed. The summer and fall of 1972 followed a relatively calm winter of light rainfall (Harger 1979: append. B), and was a favorable period for growth of small benthic algae and associated animals, which are important forage for surfperches and other microcarnivores. On the other hand, poor visibility may have caused abrupt decreases in counts of *Chromis punctipinnis* at the island site in 1973. An obligatory daytime planktivore (Bray 1978), this species may seek bottom shelter when water is turbid. Generally, midwater planktivores were more variable in numbers than other species. Decreased kelp cover at the mainland site in 1974 probably drove some fish bottomward, but not necessarily out of view; an aggregate decrease of eight individuals per canopy transect of *C. punctipinnis*, *Paralabrax clathratus*, and *O. californica* accompanied a corresponding increase of five per bottom transect.

However, less obvious factors may be more important, because other periods of clear and warm water produced no such peak abundances. Time lags in responses of fish populations to environmental change preclude simple explanations of annual variation. Lags between bumper births and subsequent adult recruitment may cause populations to overshoot their environmental carrying capacities (Hutchinson 1978). Alternatively, fixed spawning seasons coupled with an unpredictable cycle in food production may limit recruits independently of the carrying capacity of the environment for adults (Cushing 1969). From bottom-trawl catches, Mearns[12] concluded that recruitment of juvenile nearshore fishes occurs over relatively short periods off southern California and may vary markedly in success among species from one year to the next. Larson (1977) found that counts of *S. carnatus* and *S. chrysomelas* decreased significantly at several depths in an area near the island site during 1973-76. This decrease may have been the result of sparse juvenile settlement observed in 1974-75.

Migration and predation may play a role, especially at the mainland site, a semi-isolated offshore reef; e.g., kelp perch, which are canopy specialists, occurred sporadically and sparsely there. Kelp cover has varied considerably over the years. But even though cover may vary at other places as well, the distance of this reef from extensive kelp beds inshore may have inhibited kelp-perch recolonization after periods of canopy loss. Several natural predators eat reef fishes, but we do not know if the rate varies from year to year. During the day, harbor seals and sea lions forage at both sites. Predatory fish such as kelp bass may eat relatively more young of species such as surfperches that do not hide in the reef itself, during periods when plant cover is sparse. At night, larger individuals of such prey fish may be particularly vulnerable to large Pacific electric ray, *Torpedo californica*, which invade the reef then (Bray and Hixon 1978). Love (1978) concluded that olive rockfish, which grow slowly and seldom move between reefs, are decimated chronically by overfishing. Although kelp bass are equally exploited, adult replacements apparently move in to restore a portion of a contiguous population (Quast 1968d).

It is noteworthy that the constancy or "stability" in species composition of our fish assemblages was roughly correlated with species diversity. Canopy assemblages were relatively simple, with many individuals distributed unevenly among a few species. They were less constant in composition than the bottom assemblages, which were characterized by more species and more even distribution of individuals among species. Also, the island bottom assemblage, which was the more diverse

[12]Mearns, A. J. 1977. Abundance of bottom fish off Orange County. *In* Coastal water research project, annual report 1977, p. 133-142. Southern California Coastal Water Research Project, 646 W. Pacific Coast Highway, Long Beach, CA 90806.

because of greater evenness, maintained a more constant species composition than the mainland-bottom assemblage. But there is no good basis, either theoretical (May 1973) or empirical, for assuming that this relation is a causal one. Some diverse communities of coral-reef fishes are reportedly not stable at all; in fact, fluctuations in their species composition may actually increase their diversity (Sale 1977, 1978; Talbot et al. 1978).

Rather, both constancy and diversity of the assemblages are probably determined by the type of habitat in which they live. Thus, the relatively low diversity and high temporal instability of the canopy assemblages probably reflect the simplicity and instability of the canopy habitat. Most fish meet in the canopy to eat plankton or planktivorous fishes. In this way, the canopy habitat is a concourse, where animals meet for one purpose (Elton 1927; Whittaker 1965). Here there are relatively few opportunities for diversifying form and function, and hence fewer species. Relatively few environmental factors strongly influence species distributions, as May (1975) suggested in general for simply structured communities. Ephemeral currents, turbidity, temperature, and kelp growth may influence the distribution of canopy dwellers. Bray (1978) has shown that the distribution of adult blacksmith is strongly affected by food-bearing currents. Adults have largely independent sources of food and shelter: the reef provides shelter but water currents carry in their planktonic food. Blacksmith feed in dense aggregations, and since local oceanographic conditions fluctuate rapidly (Quast 1968a) and plankton occurs in patches (Wiebe 1970), the location of their optimal area of foraging frequently shifts.

In contrast, our bottom assemblages depend on more stable commodities like rocks and infaunal prey, which are not so immediately affected by factors, like currents, that change rapidly. Many bottom species are solitary, parochial, or even territorial (Clarke 1970; DeMartini 1976; Larson 1977; Hixon 1979). Thus, their local density is not so likely to change from day to day.

The greater variability of the mainland-bottom assemblage than that of the island is curious. Perhaps the relative isolation of the mainland site may contribute to vagarious settlement of fish larvae and other recruitment (Larson 1977). Also, the mainland site has relatively large areas of reef flat and a surrounding plain of sand and cobble, creating more of a "transitional" type of habitat. Periodic occurrences of such species as the black croaker, *Cheilotrema saturnum*, and rainbow surfperch, which are atypical of continuous high-relief rocky habitats, lend discontinuity to the Naples fish assemblage.

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CERATIOID ANGLERFISHES OF THE PHILIPPINE ARCHIPELAGO, WITH DESCRIPTIONS OF FIVE NEW SPECIES[1]

THEODORE W. PIETSCH[2] AND JEFFREY A. SEIGEL[3]

ABSTRACT

Ceratioid anglerfishes of the Philippine Archipelago, an area bounded by the islands of the Philippines to the north, Malaysia and Sumatra to the west, and New Guinea to the east, represent 10 of the 11 ceratioid families, 22 genera and 42 species, 5 species of which are newly described forms of the genus *Oneirodes* (Oneirodidae). The vast bulk of this material has recently been provided by midwater collections made by the *Alpha Helix* during the 1975 Southeast Asian Bioluminescence Expedition. All known records of ceratioids are listed with keys to families, genera, and species represented in the area. Revised and supplemental diagnostic and descriptive data as well as notes on geographic distribution are also provided.

Our knowledge of the ceratioid anglerfish fauna of the Philippine Archipelago, an area bounded by the islands of the Philippines to the north, Malaysia and Sumatra to the west, and New Guinea to the east, has recently been broadly expanded by midwater collections made by the RV *Alpha Helix* during the 1975 Southeast Asian Bioluminescence Expedition. This collecting effort was the first major ichthyological survey of this part of the world since the historic cruises of the United States Fisheries steamer *Albatross* in 1907-09, and the Danish RV *Dana* in 1929. The Ceratioidei are now represented by 10 of the 11 families, 22 genera, and 42 species, 5 species of which are newly described forms of the genus *Oneirodes* (Oneirodidae). All known records of ceratioids from this area are listed below with keys to families, genera, and species. Revised and supplemental diagnostic and descriptive data as well as notes on geographic distribution are also provided.

METHODS AND MATERIALS

Standard lengths (SL) are used throughout. Methods for taking counts and measurements, and terminology used in describing escal morphology follow Pietsch (1974a, fig. 60). Terminology used in describing the various parts of the angling apparatus follows Bradbury (1967). Definitions of terms used for the different stages of development follow Bertelsen (1951). Locality data for *Alpha Helix* stations that yielded ceratioid material are listed in Appendix 1. *Alpha Helix* collections were made with a rectangular midwater trawl of 8 m^2 mouth area (RMT-8) that was equipped with an opening and closing device. This gear is more fully described elsewhere (Clarke 1969; Baker et al. 1973; Hopkins et al. 1973). All *Alpha Helix* material was deposited in the Natural History Museum of Los Angeles County (LACM). Material from other sources is catalogued in the following institutions: Australian Museum, Sydney (AMS), Scripps Institution of Oceanography, La Jolla (SIO), National Museum of Natural History, Washington, D.C. (USNM), and the Zoological Museum, University of Copenhagen (ZMUC). Specimens are females unless otherwise stated.

KEY TO FEMALES OF THE FAMILIES OF SOUTHEAST ASIAN CERATIOIDEI

1A. No distal bulb, illicium tipped with filaments; longest rays of dorsal and anal fin >60% of SL ..... Caulophrynidae
1B. A bulbose light organ on tip of illicum; longest rays of dorsal and anal fin much <60% SL 2
2A. More than 11 dorsal fin rays .... Melanocetidae
2B. Less than 11 dorsal fin rays 3
3A. Two or three caruncles on back; cleft of mouth vertical to very oblique . Ceratiidae

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3B. No caruncles on back; cleft of mouth nearly horizontal 4
4A. A second cephalic ray present immediately posterior to base of illicium, bearing a distal luminous gland (withdrawn beneath skin in larger specimens, its presence indicated by a small pore) ..... Diceratiidae
4B. No second cephalic ray 5
5A. Upper jaw extending anteriorly far beyond lower jaw; esca with 1-3 denticles ..... Thaumatichthyidae
5B. Jaws equal anteriorly; esca without denticles 6
6A. Illicium emerging on tip of snout; length of head <35% SL; length of caudal peduncle >20% SL; 5 pectoral radials ..... Gigantactinidae
6B. Illicium emerging behind tip of snout; length of head >35% SL; length of caudal peduncle <20% SL; 3 or 4 pectoral radials 7
7A. Dermal spines or plates present 8
7B. Skin naked 10
8A. Skin with some large, bony plates, each bearing a median spine ..... Himantolophidae
8B. Skin with numerous, close set spines .. 9
9A. Teeth present on ceratobranchials 1-4; 4 pectoral radials (but fusing to 3 in specimens greater than about 150 mm SL); larvae and adolescents up to about 50 mm SL with a short, digitiform, hyoid barbel ..... Centrophrynidae
9B. Ceratobranchial teeth absent; 3 pectoral radials; no hyoid barbel ..... Oneirodidae (*Spiniphryne*)
10A. Six branchiostegal rays; more than 4 dorsal fin rays; anal fin rays 4-7 ..... Oneirodidae
10B. Four to five branchiostegal rays; 3 dorsal fin rays, rarely 2 or 4; anal fin rays 2-4 ..... Linophrynidae

CAULOPHRYNIDAE

Key to Females of Genera and Species of Southeast Asian Caulophrynidae

1A. Illicium short, less than SL; dorsal fin rays 14-22; anal fin rays 12-19 ..... *Caulophryne pelagica* (Brauer)
1B. Illicium long, 268% of SL in a 41 mm SL specimen; dorsal fin rays 6, anal fin rays 5 ..... *Robia legula* Pietsch (known from only the holotype, 41 mm SL)

Caulophryne Goode and Bean 1896

Caulophryne pelagica (Brauer 1902)

Material.—LACM 36023-1, 13 mm SL, stn 143.

A single individual, representing the sixth known specimen of *C. pelagica*, and the first record of this species from southeast Asian waters, was collected by the *Alpha Helix* in 1975. It was included in a recent revision of the family (Pietsch 1979).

Caulophryne sp. A

Material.—LACM 36025-1, female 98 mm SL with parasitic male 12 mm SL, stn 37.

This female and parasitically attached male, collected from the Banda Sea, cannot be placed within the material of any of the three recognized species of *Caulophryne* (Pietsch 1979). The attached male represents the second example of sexual parasitism in the family Caulophrynidae.

Caulophryne sp. B, Figure 1

Material.—LACM 36112-1, 10 mm SL, stn 183; LACM 36111-1, 10.5 mm SL, stn 184; LACM 36109-2, 11.5 mm SL, stn 193.

These three small females were sorted out of the *Alpha Helix* collections after a recent revision of the family went to press (Pietsch 1979). They differ significantly from the material of the three recognized species of *Caulophryne* in having an elongate, distally branched, lateral appendage on each side of the escal bulb; distal escal filaments, present in all the described species of the genus, are absent. Although these most likely represent a new form, the small size of the specimens and their poor condition do not warrant description at this time.

Robia Pietsch 1979

Robia legula Pietsch 1979

Material.—LACM 36024-1, 41 mm, stn 81 (holotype).

This species is known from a single specimen collected in the Banda Sea (Pietsch 1979).

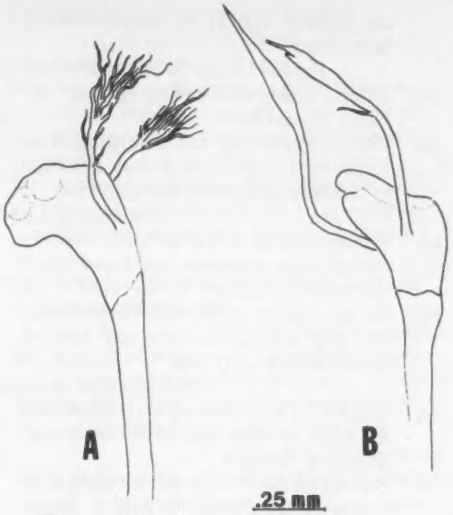


FIGURE 1.—Escae of *Caulophryne* sp. B, left lateral views: A. LACM 36112-1, 10 mm SL; B. LACM 36111-1, 10.5 mm SL.

MELANOCETIDAE

Melanocetus Günther 1864

Key to Females of Species of Southeast Asian *Melanocetus*

1A. Anterior margin of vomer nearly straight; width of pectoral fin lobe 10.7-17.8% SL; number of lower jaw teeth 32-78 .... *M. johnsoni* Günther

1B. Anterior margin of vomer deeply concave; width of pectoral fin lobe 6.1-8.9% SL; number of lower jaw teeth 46-142 .... *M. murrayi* Günther

Melanocetus johnsoni Günther 1864

Material.—LACM 36076-3, 14 mm SL, stn 26; LACM 36059-3, 15 mm SL, stn 103; LACM 36032-3, 15 mm SL, stn 110; LACM 36076-5, 17 mm SL, stn 26; LACM 36074-2, 18 mm SL, stn 120; LACM 36033-2, 36 mm SL, stn 88.

Six specimens of *M. johnsoni* were collected by the *Alpha Helix* in 1975, all of which were included in a recent revision of the Melanocetidae (Pietsch and Van Duzer 1980). This species has a wide geographic distribution in tropical and subtropical waters of all three major oceans of the world.

Melanocetus murrayi Günther 1887

Material.—LACM 36114-1, 68 mm SL, stn 66; LACM 36113-1, 82 mm SL, stn 71; LACM 36115-1, 84 mm SL, stn 102.

Melanocetus murrayi is represented by three females in the *Alpha Helix* collections (Pietsch and Van Duzer 1980). This species has a wide horizontal distribution in the Atlantic and Pacific Oceans, but is apparently absent from the Indian Ocean.

Melanocetus sp.

Material.—Males: LACM 36067-2, 13.5 mm SL, stn 23; LACM 36116-1, 21.5 mm SL, stn 84; LACM 36032-4, 22.5 mm SL, stn 110.

These male specimens could not be satisfactorily identified to species (Pietsch and Van Duzer 1980).

HIMANTOLOPHIDAE

Himantolophus Reinhardt 1837

Himantolophus sp.

Material.—Female: LACM 36038-3, 2(12.5-14 mm SL), stn 87. Males: LACM 36091-4, 16 mm SL, stn 142; LACM 36057-4, 19 mm SL, stn 93; LACM 36075-4, 4(19.5-21 mm SL), stn 121; LACM 36074-3, 21 mm SL, stn 120; LACM 36040-3, 27.5 mm SL, stn 27; LACM 36046-8, 2(29.5-33 mm SL), stn 97; LACM 36124-1, 31 mm SL, stn 112.

Thirteen specimens of *Himantolophus* were collected by the *Alpha Helix* from the Banda, Ceram, and Halmahera Seas. The genus is cosmopolitan in all three major oceans of the world (Bertelsen 1951), yet no adult females have been collected in the immediate area. These males and larval females could not be identified specifically.

DICERATIIDAE

Key to Genera and Species of Southeast Asian Diceratiidae

1A. Illicium <50% SL; distance between insertion of illicium and symphysial car-

tilage of upper jaw <15% SL .... *Diceratias bispinosus* (Günther)

1B. Illicium >80% SL; distance between insertion of illicium and symphysial cartilage of upper jaw >30% SL .... *Phrynichthys thele* Uwate

Diceratias Günther 1887

Diceratias bispinosus (Günther 1887)

Material.—LACM 36075-1, 20 mm SL, stn 121.

A single specimen of *Diceratias bispinosus* was collected by the *Alpha Helix* in the Halmahera Sea. This species is known only from the Indo-West Pacific (Uwate 1979).

Phrynichthys Pietschmann 1926

Phrynichthys thele Uwate 1979

Material.—LACM 36077-1, 32 mm SL, stn 155 (holotype); LACM 36076-1, 22 mm, stn 26 (paratype).

This species is known only from two specimens collected from the Ceram and Halmahera Seas, and described in a recent revision of the Diceratiidae (Uwate 1979).

ONEIRODIDAE

Key to Females of Genera of Southeast Asian Oneirodidae

1A. Skin covered with numerous, close set spines ..... *Spiniphryne* Bertelsen

1B. Skin naked 2

2A. Sphenotic spines present; opercle deeply notched posteriorly 3

2B. Sphenotic spines absent; opercle only slightly concave posteriorly .... *Chaenophryne* Regan

3A. Pectoral fin lobe short and broad, shorter than longest pectoral fin rays 4

3B. Pectoral fin lobe long and narrow, longer than longest pectoral fin rays .... *Chirophryne* Regan and Trewavas

4A. Lower jaw with a symphysial spine, ventral margin of dentaries at symphysis convex; caudal fin rays not internally pigmented 5

4B. Lower jaw without symphysial spine, ventral margin of dentaries at symphysis concave; caudal fin rays internally pigmented .... *Pentherichthys* Regan and Trewavas

5A. Illicial apparatus emerging from between frontal bones 6

5B. Illicial apparatus not emerging from between frontal bones but between sphenotic spines or further posterior .. .. *Lophodolos* Lloyd

6A. Dorsal margin of frontal bones strongly curved; subopercle short and broad, lower part nearly circular 7

6B. Dorsal margin of frontal bones nearly straight; subopercle long and narrow, lower part strongly oval .... *Dolopichthys* Garman

7A. Caudal fin rays covered with black skin for some distance beyond fin base; anal fin rays 5, rarely 4 8

7B. Caudal fin rays not coverd by black skin except at base; anal fin rays 4, rarely 5 ..... *Oneirodes* Lütken

8A. Cleft of mouth extending past eye; length of escal bulb more than half length of illicial bone; upper part of subopercle broad and rounded .... *Microlophichthys* Regan and Trewavas

8B. Cleft of mouth not extending past eye; escal bulb considerably shorter than half length of illicial bone; upper part of subopercle slender and tapering to a point ..... *Danaphyrne* Bertelsen

Spiniphryne Bertelsen 1951

Spiniphryne gladisfenae (Beebe 1932)

Material.—LACM 36073-2, 18 mm SL, stn 94.

Spiniphryne gladisfenae was previously known only from the Atlantic Ocean (Bertelsen and Pietsch 1975): three specimens collected from the eastern tropical Atlantic, and the holotype from off Bermuda. A fifth specimen, collected in the Banda Sea by the *Alpha Helix*, is the first record from the Pacific.

Oneirodes Lütken 1871

Key to Females of Species of Southeast Asian *Oneirodes*

Oneirodes melanocauda, known only from five larval specimens is omitted from the following key.

1A. Epibranchial of first arch toothed .... *O. carlsbergi* (Regan and Trewavas)
1B. Epibranchial teeth absent 2
2A. Anterior escal appendage without internal pigment; usually two pairs of filamentous anterolateral escal appendages ..... (*O. schmidti* group) .. 3
2B. Anterior escal appendage internally pigmented; anterolateral escal appendages, if present, one or four filamentous pairs 5
3A. Length of all escal appendages less than length of escal bulb .... *O. micronema* Grobecker
3B. Length of some escal appendages much greater than length of escal bulb 4
4A. Anterior escal appendage unbranched, anterolateral escal appendages absent .. .. *O. alius* Seigel and Pietsch
4B. Anterior escal appendage highly branched, anterolateral escal appendages present .. *O. schmidti* (Regan and Trewavas)
5A. Medial escal appendages present 6
5B. Medial escal appendages absent 10
6A. Posterior escal appendage cylindrical in cross section 7
6B. Posterior escal appendage compressed .. 8
7A. Anterior escal appendage cylindrical in cross section; posterior escal appendage as long as or longer than length of escal bulb ..... *O. eschrichtii* Lütken
7B. Anterior escal appendage laterally compressed; posterior escal appendage less than half length of escal bulb .... *O. sabex* n.sp.
8A. Medial escal appendages short and closely set in a tight cluster 9
8B. Medial escal appendages elongate and widely placed ..... *O. thysanema* n.sp
9A. Anterior escal appendage elongate and cylindrical in cross section, with a few short, distal branches; pectoral fin rays 17 ..... *O. pterurus* n.sp.
9B. Anterior escal appendage short and laterally compressed, with a membranous scalloped distal margin; pectoral fin rays 13 or 14 .... *O. cristatus* (Regan and Trewavas)
10A. Anterior escal appendage directed dorsally; posterior escal appendage as long as or longer than length of escal bulb ...11
10B. Anterior escal appendage directed anteroventrally; posterior escal appendage much shorter than length of escal bulb ..... *O. plagionema* n.sp.
11A. Posterior escal appendage unbranched, length two to four times length of escal bulb .. *O. flagellifer* (Regan and Trewavas)
11B. Posterior escal appendage branched, approximately as long as length of escal bulb ..... *O. schistonema* n.sp.

Oneirodes carlsbergi **(Regan and Trewavas 1932)**

Material.—LACM 36068-2, 19 mm, stn 25.

Oneirodes carlsbergi is known from the western tropical Atlantic and Pacific Oceans, and from a single record in the Indo-West Pacific region at about lat. 17° N, long. 120° E (Pietsch 1974a, fig. 107). An additional specimen, collected by the *Alpha Helix* from the Banda Sea, is the second known record from this part of the world.

Oneirodes cristatus **(Regan and Trewavas 1932), Figure 2**

Oneirodes cristatus is known only from the type material (3 females, 20-165 mm SL) collected by the *Dana* in the Banda and Celebes Seas (Pietsch 1974a).

Oneirodes eschrichtii **Lütken 1871, Figure 3**

Material.—LACM 36049-1, 10.5 mm SL, stn 194; LACM 36122-2, 12 mm SL, stn 179; LACM 36121-2, 21 mm SL, stn 178.

Oneirodes eschrichtii has a nearly cosmopolitan

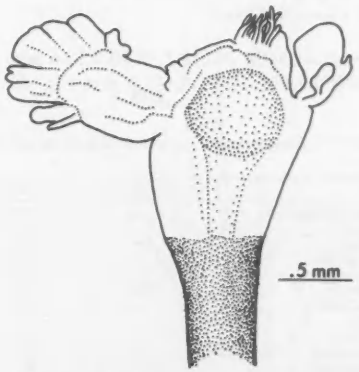


FIGURE 2.—Esca of *Oneirodes cristatus*, lectotype, ZMUC P9286, 165 mm SL, left lateral view.

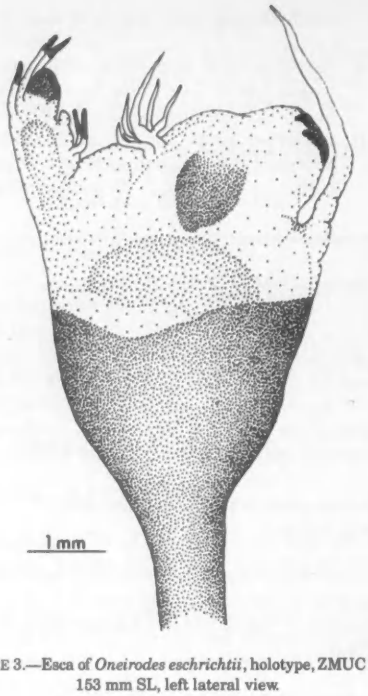


FIGURE 3.—Esca of *Oneirodes eschrichtii*, holotype, ZMUC P64, 153 mm SL, left lateral view.

distribution (Pietsch 1974a, fig. 109). Three specimens of this species were collected by the *Alpha Helix* in southeast Asian waters.

Oneirodes flagellifer (Regan and Trewavas 1932), Figure 4, Table 1

Material.—LACM 36118-1, 2(10.5-13.5 mm SL), stn 180; LACM 36117-1, 11.5 mm SL, stn 173;

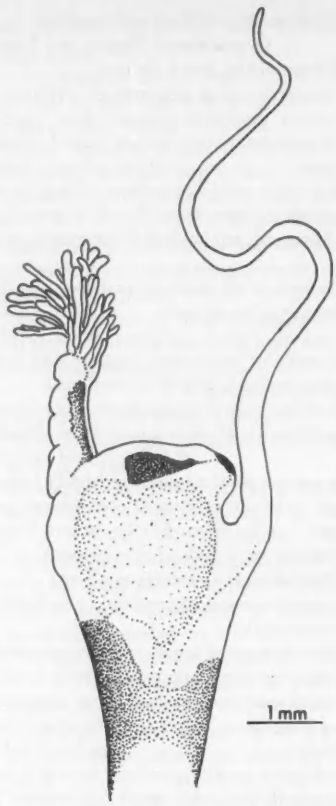


FIGURE 4.—Esca of *Oneirodes flagellifer*, holotype, ZMUC P9280, 22 mm SL, left lateral view.

LACM 36100-2, 12 mm SL, stn 166; LACM 36112-2, 14 mm SL, stn 183; LACM 36109-3, 15.5 mm SL, stn 193.

TABLE 1.—Measurements and counts of specimens of *Oneirodes flagellifer*. Measurements expressed as percentage of standard length.

Item	LACM 36118-1	LACM 36117-1	LACM 36100-2	LACM 36118-1	LACM 36112-2	LACM 36109-3
Standard length (mm)	10.5	11.5	12	13.5	14	15.5
Length:						
Head	—	43.5	41.7	46.1	46.4	45.2
Lower jaw	—	47.8	45.8	46.1	50.0	48.4
Premaxilla	—	34.8	33.3	37.0	35.7	32.3
Illicium	23.8	21.7	—	22.2	25.0	19.3
Head depth	—	43.5	41.7	37.0	46.4	45.2
Teeth:						
Vomer	4	6	6	6	6	7
Upper jaw	16	19	17	28	42	42
Lower jaw	22	30	28	36	45	48
Dorsal fin rays	—	6	5	5	5	5
Anal fin rays	4	4	4	—	4	4
Pectoral fin rays	—	—	15	15	15	14

Oneirodes flagellifer was previously known from only three specimens, all collected from the Indo-West Pacific region: the holotypes of *O. flagellifer* and *O. thysanophorus* (= *O. flagellifer*) collected by the *Dana* in 1929, and an additional specimen collected by the *Galathea* in 1951 (Pietsch 1974a, fig. 110). The *Alpha Helix* has added six additional females from the Sulu Sea that compare very well with the previously recorded material (Table 1).

Oneirodes melanocauda Bertelsen 1951

Oneirodes melanocauda is known from five larval specimens (easily separated from other *Oneirodes* larvae by the presence of pigment on the tips of the caudal fin rays, Pietsch 1974a) three of which were collected by the *Dana* in southeast Asian waters. No additional material was provided by the Southeast Asian Bioluminescence Expedition.

Oneirodes plagionema n.sp., Figures 5, 6; Table 2

Material.—A single female, the holotype, LACM 36114-2, 25 mm SL, stn 66.

Diagnosis.—A species of *Oneirodes* differing from all previously described species in escal morphology: anterior appendage narrow, elongate, and directed anteroventrally; medial appendages absent; posterior appendage minute; a pair of filamentous, branched, anterolateral appendages.

Description.—Escal appendage pattern B (Pietsch 1974a, fig. 60B); esca with anterior appendage narrow and elongate, with a single, short, distal filament, directed anteroventrally; medial appendages absent; terminal papilla unusually large, rounded, with a distal pigment spot; posterior appendage minute; a filamentous, branched, anterolateral appendage on each side (Figure 5).

Suboperculum short, upper end rounded without indentation on posterior margin (Figure 6); length of lower fork of operculum 24.0% of SL; ratio of lengths of upper and lower forks of operculum 0.53.

Epibranchial teeth absent; teeth present on pharyngobranchial II.

Counts and measurements in Table 2.

Etymology.—The name *plagionema* is derived from the Greek *plagios*, meaning oblique, and *nema*, thread, alluding to the oblique, anteroventrally directed anterior escal appendage.

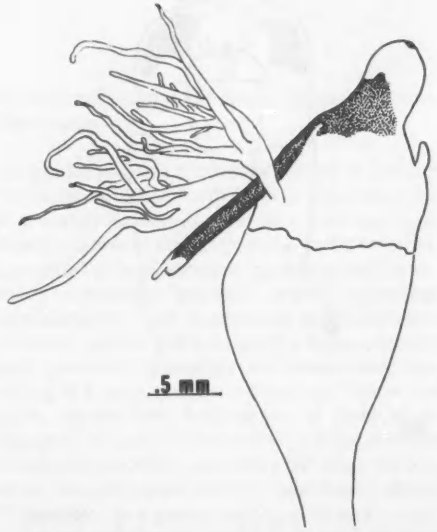


FIGURE 5.—Esca of *Oneirodes plagionema* n.sp., holotype, LACM 36114-2, 25 mm SL, left lateral view.

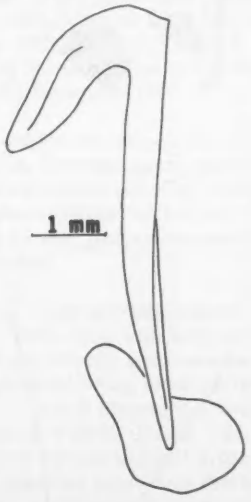


FIGURE 6.—Opercular bones of *Oneirodes plagionema* n.sp., holotype, LACM 36114-2, 25 mm SL, right lateral view.

TABLE 2.—Measurements and counts of four new species of *Oneirodes*. Measurements expressed as percentage of standard length.

Item	*O. plagioneme* Holotype LACM 36114-2	*O. pterurus* Holotype LACM 36075-3	*O. schistoneme* Holotype LACM 36036-3	*O. thysanema* Paratype LACM 36073-4	*O. thysanema* Holotype USNM 207931
Standard length (mm)	24	30	74	13	26.5
Length:					
Head	45.8	46.7	37.2	38.5	45.3
Lower jaw	45.8	50.0	41.2	42.3	47.2
Premaxilla	31.2	35.0	26.3	26.9	30.2
Illicium	25.0	26.7	28.4	15.4	26.4
Head depth	37.5	46.7	28.4	34.6	43.4
Teeth:					
Vomer	5	6	6	4	6
Upper jaw	24	30	42	8	32
Lower jaw	35	39	40	10	30
Dorsal fin rays	5	6	6	5	6
Anal fin rays	4	4	4	4	4
Pectoral fin rays	15	17	14	17	17

Oneirodes pterurus n.sp., Figures 7, 8; Table 2

Material.—A single female, the holotype, LACM 36075-3, 30 mm SL, stn 121.

Diagnosis.—A species of *Oneirodes* differing from all previously described species in escal morphology: anterior appendage with a few distal branches; medial appendage represented by a tuft

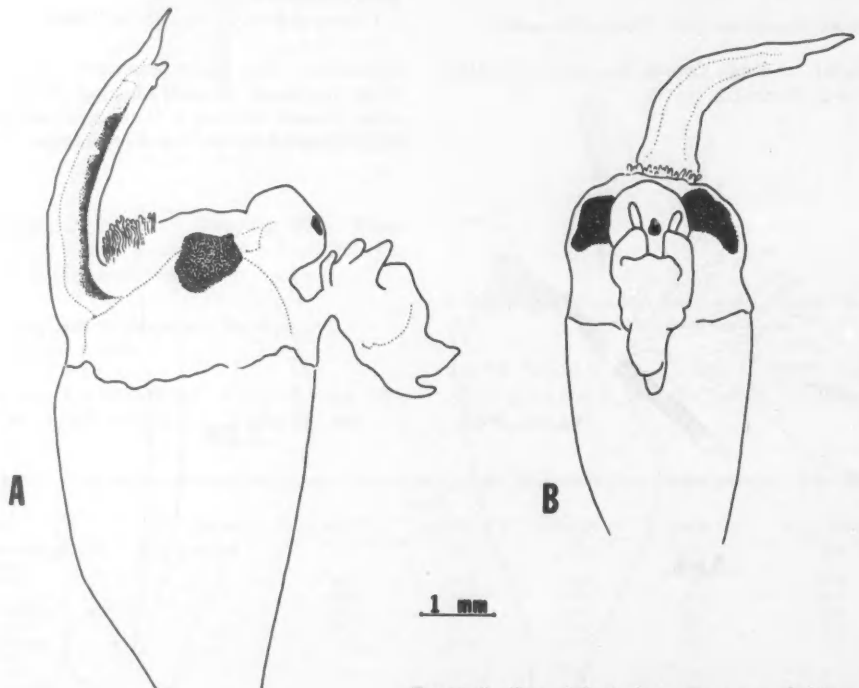


FIGURE 7.—Esca of *Oneirodes pterurus* n.sp., holotype, LACM 36075-3, 30 mm SL: A. Left lateral view. B. Posterior view.

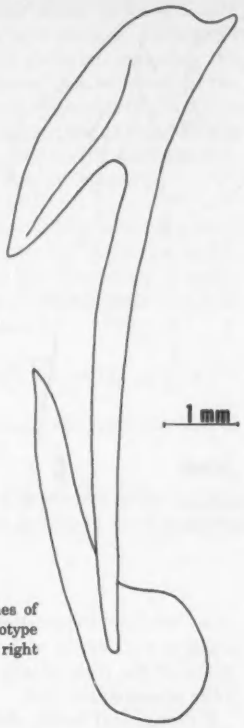


FIGURE 8.—Opercular bones of *Oneirodes pterurus* n.sp., holotype LACM 36075-3, 30 mm SL, right lateral view.

of short filaments; posterior appendage nonfilamentous.

Description.—Escal appendage pattern B (Pietsch 1974a, fig. 60B); esca with anterior appendage approximately as long as escal bulb, bearing three, short branches at distal tip; distal end of internal, pigmented tube of anterior appendage with a circular, translucent "eye-spot"; medial appendage represented by a tuft of extremely short filaments; terminal papilla bulbous, with a distal pigment spot; posterior appendage nonfilamentous, consisting of a large, compressed wedge of tissue on a short, narrow base, bearing two or three, short filaments on each side of anterior surface, and two winglike projections, one above the other, on posterior margin; anterolateral appendages absent (Figure 7).

Suboperculum unusually long and narrow, upper end tapering to a point without indentation on posterior margin (Figure 8); length of lower fork of operculum 27.3% of SL; ratio of lengths of upper and lower forks of operculum 0.56.

Epibranchial teeth absent; teeth present on pharyngobranchial II.

Counts and measurements in Table 2.

Etymology.—The name *pterurus* is derived from the Greek *pteron*, meaning wing, and *ura*, tail, alluding to the winglike posterior escal appendage of this species.

Oneirodes sabex n.sp., Figures 9, 10; Table 3

Oneirodes eschrichtii Pietsch 1974a:100, 103, fig. 116B (misidentification).

Material.—Fourteen metamorphosed females, 12-121 mm. Holotype: LACM 36116-3, 46 mm SL, stn 84. Paratypes: LACM 36087-4, 3(12-26.5 mm SL), stn 135; LACM 36068-3, 12 mm SL, stn 25; LACM 36028-5, 13 mm SL, stn 141; LACM 36023-3, 13 mm SL, stn 143; LACM 36089-4, 2(15-17 mm SL), stn 137; LACM 36051-3, 15 mm SL, stn 38; LACM 36088-4, 15.5 mm SL, stn 136; AMS I.20315-010, 32.5 mm SL, *Kapala*, lat. 33°53′ S, long. 152°02′ E, Engel Midwater Trawl, 0-900 m, bottom depth 1,800 m, 1330-1990 h, 14 December 1977; AMS I.20314-016, 39 mm SL, *Kapala*, lat. 33°28′ S, long. 152°33′ E, Engel Midwater Trawl, 0-900 m, bottom depth 4,200 m, 0530-1045 h, 14 December 1977; SIO 70-339, 121 mm SL, lat. 19°35′ N, long. 122°57′ E, 3 m IKMT (Isaacs-Kidd Midwater Trawl), 0-1,450 m, 1845-0225 h, 15-16 September 1970.

Diagnosis.—A species of *Oneirodes* differing from all previously described species in escal morphology: anterior appendage noncylindrical, compressed, without pigmented, internal tube; medial appendage present; posterior appendage cylindrical, unbranched.

Description.—Escal appendage pattern B (Pietsch 1974a, fig. 60B); esca with anterior appendage noncylindrical, strongly compressed and rounded, darkly pigmented along distal margin in some specimens; a pair of filamentous medial appendages; terminal papilla usually with two distal pigment spots situated on midline, one just behind the other; posterior appendage short, stout, and cylindrical; anterolateral appendages absent (Figure 9; Pietsch 1974a, fig. 116B).

Suboperculum short, upper end tapering to a

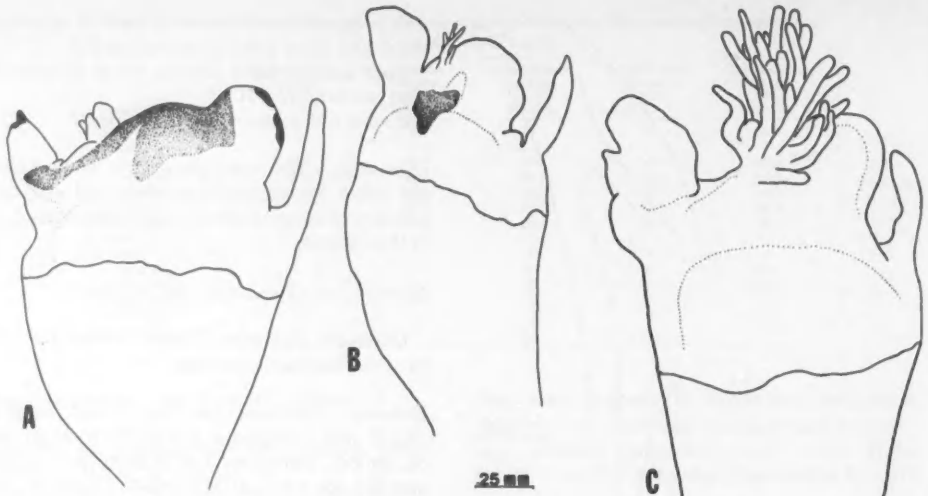
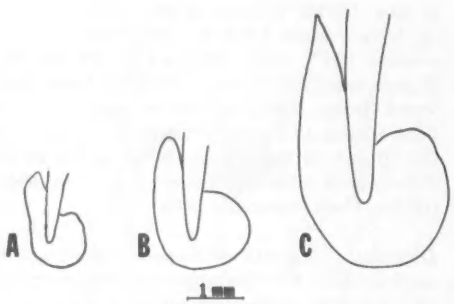


FIGURE 9.—Escae of *Oneirodes sabex* n.sp., left lateral views: A. Paratype, LACM 36089-4, 17 mm SL; B. Paratype, LACM 36087-4, 26.5 mm SL; C. Holotype, LACM 36116-3, 46 mm SL.



point without indentation on posterior margin (Figure 10); length of lower fork of operculum 27.1% of SL; ratio of lengths of upper and lower forks of operculum 0.48.

Epibranchial teeth absent; teeth present on pharyngobranchial II.

Counts and measurements in Table 3.

FIGURE 10.—Subopercula of *Oneirodes sabex* n.sp., right lateral views: A. Paratype, LACM 36089-4, 17 mm SL; B. Paratype, AMS I.20315-010, 32 mm SL; C. Holotype, LACM 36116-3, 46 mm SL.

TABLE 3.—Measurements and counts of specimens of *Oneirodes sabex* n.sp. Measurements expressed as percentage of standard length.

Item	LACM 36068-3	LACM 36028-5	LACM 36087-4	LACM 36089-4	LACM 36051-3	LACM 36088-4	LACM 36089-4	Paratype LACM 36087-4	Holotype LACM 36116-3	Paratype SIO 70-339
Standard length (mm)	12	13	13	15	15	15.5	17	26.5	45.5	121
Length:										
Head	41.7	46.1	38.5	43.3	40.0	41.9	35.3	39.5	37.4	35.1
Lower jaw	45.8	42.3	42.3	46.7	43.3	48.4	35.3	45.3	41.8	36.7
Premaxilla	29.2	30.8	30.8	33.3	30.0	32.3	23.5	32.1	27.5	26.0
Illicium	20.8	19.2	19.2	26.7	23.3	29.0	17.6	26.5	18.7	14.4
Head Depth	41.7	38.5	38.5	43.3	40.0	45.2	35.3	41.5	38.5	34.2
Teeth:										
Vomer	4	4	4	5	4	6	4	6	6	6
Upper jaw	5	15	—	22	23	34	25	30	26	42
Lower jaw	5	26	21	30	30	34	25	37	41	50
Dorsal fin rays	6	5	6	6	6	6	6	5	6	6
Anal fin rays	4	4	4	4	4	4	4	4	4	4
Pectoral fin rays	—	16	16	15	15	16	17	15	14	16

Distribution.—*Oneirodes sabex* is known only from southeast Asian and eastern Australian waters: the *Alpha Helix* material, including the holotype and 10 paratypes, was collected in the Banda Sea; the 121 mm SL paratype (SIO 70-339) is from off Luzon, Philippines; the 32.5 and 39 mm SL paratypes (AMS I. 20315-010, AMS I.20314-016) were collected off Sydney, Australia.

Etymology.—The name *sabex* is an acronym formed from the initial letters of the name "Southeast Asian Bioluminescence Expedition" in recognition of the important ichthyological contribution made by those involved.

Oneirodes schistonema n.sp., Figures 11, 12; Table 2

Material.—A single female, the holotype, LACM 36036-3, 74 mm, stn 24.

Diagnosis.—A species of *Oneirodes* differing from all previously described species in escal morphology: anterior appendage branched, unpigmented internally; medial and anterolateral appendages absent; posterior appendage branched.

Description.—Escal appendage pattern B (Pietsch 1974a, fig. 60B); esca with a stout, unpigmented, anterior appendage, less than length of escal bulb, bearing four, short, distal branches; pigmented internal tube of anterior appendage absent; medial and anterolateral appendages absent; terminal papilla without distal pigment spot; posterior appendage as large as anterior appendage, bearing four short branches near distal end (Figure 11).

Upper end of suboperculum long, narrow, and tapering, left suboperculum deeply indented (Figure 12); length of lower fork of operculum 25.3% of SL; ratio of lengths of upper and lower forks of operculum 0.48.

Epibranchial teeth absent; teeth present on pharyngobranchial II.

Counts and measurements in Table 2.

Etymology.—The name *schistonema* is derived from the Greek *schistos*, meaning divided, and *nema*, thread, alluding to the divided anterior and posterior escal appendages of this species.

Oneirodes thysanema n.sp., Figures 13, 14; Table 2

Material.—Two females, 13 and 26.5 mm SL. Holotype: USNM 207931, 26.5 mm SL; Ocean Acre cruise 7, stn 13N, Bermuda, lat. 32°18′ N, long. 63°30′ W, 3 m IKMT, 0-1,500 m, 1430-1730 h, 8

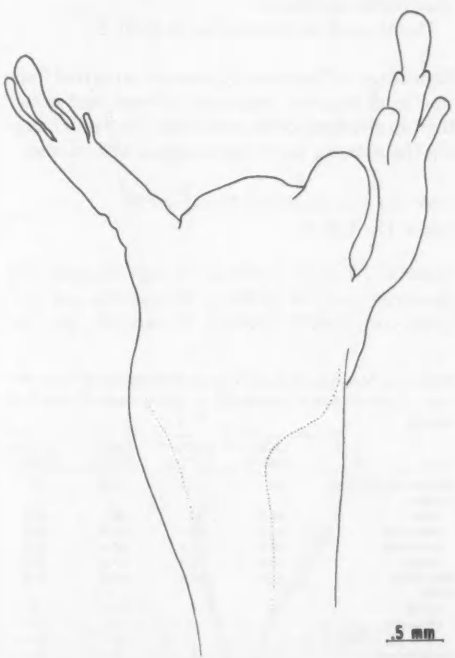


FIGURE 11.—Esca of *Oneirodes schistonema* n.sp., holotype, LACM 36036-3, 74 mm SL, left lateral view.

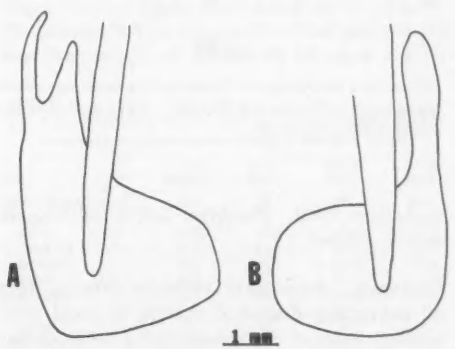


FIGURE 12.—Subopercle of *Oneirodes schistonema* n.sp., holotype, LACM 36036-3, 74 mm SL: A. Right lateral view; B. Left lateral view.

FIGURE 13.—Esca of *Oneirodes thysanema* n.sp., USNM 207931, holotype, 26.5 mm SL, left lateral view.

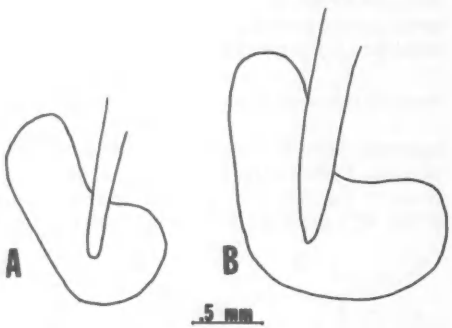


FIGURE 14.—Subopercula of *Oneirodes thysanema* n.sp., right lateral views: A. Paratype, LACM 36093-4, 13 mm SL; B. Holotype, USNM 207931, 26.5 mm SL.

September 1969. Paratype: LACM 36073-4, 13 mm SL, stn 94.

Diagnosis.—A species of *Oneirodes* differing from all previously described species in escal morphology: anterior appendage with a series of filaments along posterior margin; medial appendages in three groups; terminal papilla elongate; posterior appendage compressed and branched.

Description.—Escal appendage pattern B (Pietsch 1974a, fig. 60B); esca with a stout, internally pigmented, anterior appendage, greater than length of escal bulb, bearing along posterior margin a single branched filament proximally, and a series of unbranched filaments distally; medial appendages in three groups, a highly filamentous pair lying between a similar, but unpaired appendage, and a series of three, stout papillae situated at the base of the terminal papilla; terminal papilla unusually long, directed posterodorsally; posterior appendage as long as anterior appendage, highly compressed, bearing one or two, short, lateral filaments, and a considerably longer, branched, filamentous, anterolateral appendage on each side; distal tip of internal tube of anterior appendage, and dorsal pigment patch of escal bulb with a paired circular, translucent "eye spot" (Figure 13).

Suboperculum short and broad, upper end rounded without indentation on posterior margin (Figure 14); length of lower fork of operculum 27.7-30.2% of SL; ratio of lengths of upper and lower forks of operculum 0.48-0.50.

Epibranchial teeth absent; teeth present on pharyngobranchial II.

Counts and measurements in Table 2.

Etymology.—The name *thysanema* is derived from the Greek *thysanos*, meaning a fringe, and *nema*, thread, alluding to the numerous filaments fringing the anterior escal appendage of this species.

Oneirodes alius **Seigel and Pietsch 1978,**
Figure 15, Table 4

Material.—LACM 36026-1, 38 mm SL, stn 122 (holotype); LACM 36027-1, 18 mm SL, stn 147 (paratype); LACM 36028-1, 21 mm SL, stn 141

TABLE 4.—Measurements and counts of specimens of *Oneirodes alius*. Measurements expressed as percentage of standard length.

Item	LACM 36089-2	LACM 36091-2	LACM 36091-2	LACM 36096-2
Standard length (mm)	10	11.5	11.5	12
Length:				
Head	45.0	39.1	39.1	37.5
Lower jaw	40.0	43.5	43.5	45.8
Premaxilla	20.0	21.7	26.1	25.0
Illicium	20.0	17.4	17.4	16.7
Head depth	40.0	34.8	34.8	33.3
Teeth:				
Vomer	4	4	4	4
Upper jaw	—	—	—	14
Lower jaw	—	—	18	16
Dorsal fin rays	5	5	7	6
Anal fin rays	4	4	4	4
Pectoral fin rays	15	—	15	16

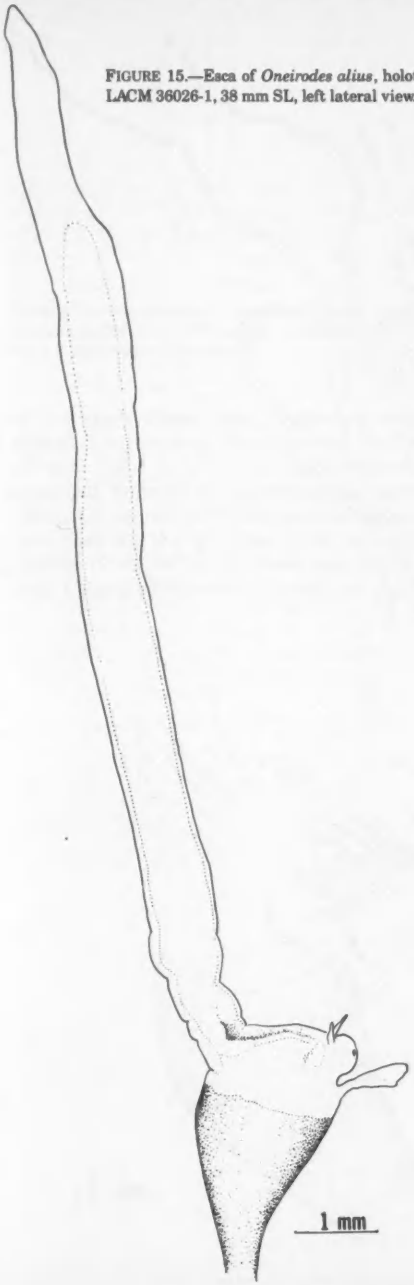


FIGURE 15.—Esca of *Oneirodes alius*, holotype, LACM 36026-1, 38 mm SL, left lateral view.

(paratype); LACM 36089-2, 10 mm SL, stn 137; LACM 36091-2, 2(11.5 mm SL), stn 142; LACM 36096-2, 12 mm SL, stn 150.

Oneirodes alius, a member of the *O. schmidti* group (Pietsch 1974a), was originally described from three specimens collected by the *Alpha Helix* in the Halmahera Sea (Seigel and Pietsch 1978). After the description went to press, four additional specimens were sorted out from *Alpha Helix* stations made in approximately the same localities as the type-material. In all respects, these specimens compare well with the original description.

Oneirodes schmidti (Regan and Trewavas 1932), Figures 16, 17; Table 5

Material.—LACM 36031-3, 15.5 mm SL, stn 58; LACM 36057-3 2(65-92 mm SL), stn 93; LACM 36067-3, 78 mm SL, stn 23.

The 1975 Southeast Asian Bioluminescence Expedition of the *Alpha Helix* provided the first representatives of *O. schmidti* since the capture of the holotype by the *Dana* in 1929. The new material compares well with the type-specimen in all characters, except for some minor differences in escal morphology. The species is redescribed below based on the new *Alpha Helix* material.

Description.—Escal appendage pattern C (Pietsch 1974a, fig. 60C); esca with a large, complex anterior appendage consisting of a wide, compressed base bearing a relatively short, unpaired and branched filament on posterior margin, two extremely long, distal filaments (about 16.3 to 17.3% of SL) that bifurcate as many as five times, and a stout, bifurcated, medial filament each branch of which becomes highly branched distally; a pair of filamentous, highly branched, medial appendages less than length of escal bulb; terminal papilla

TABLE 5.—Measurements and counts of *Oneirodes schmidti*. Measurements expressed as percentage of standard length.

Item	LACM 36031-3	LACM 36067-3	LACM 36057-3	LACM 36057-3
Standard length (mm)	15.5	78	92	65
Length:				
Head	45.2	44.9	46.2	47.7
Lower jaw	51.7	51.3	52.7	52.3
Premaxilla	38.7	35.9	36.4	40.0
Illicium	35.5	107.7	91.3	87.7
Head depth	38.7	46.1	42.4	46.1
Teeth:				
Vomer	4	6	5	5
Upper jaw	29	66	67	62
Lower jaw	36	57	56	65
Dorsal fin rays	6	6	5	6
Anal fin rays	4	4	4	4
Pectoral fin rays	16	16	17	16

FIGURE 16.—Esca of *Oneirodes schmidti*, LACM 36057-3, 65 mm SL, left lateral view.

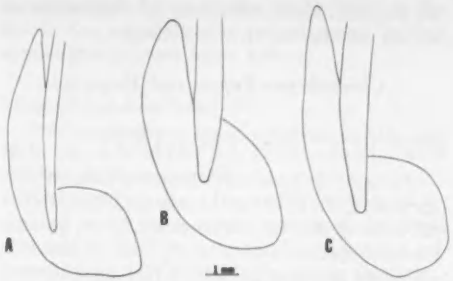


FIGURE 17.—Subopercula of *Oneirodes schmidti*, right lateral views: A. LACM 36057-3, 65 mm SL; B. LACM 36067-3, 78 mm SL; C. LACM 36057-3, 92 mm SL.

with a single, distal streak of pigment; a slender, unbranched posterior appendage less than length of escal bulb; a relatively short, filamentous, branched, anterolateral appendage on each side (the inner pair of stout, anterolateral appendages described for the holotype of *O. schmidti* by Pietsch 1974a: 78, fig. 99, correspond to the elongate, bifurcated filaments that are associated with the anterior appendage of the new material; Figure 16).

Suboperculum long and narrow, upper part tapering without indentation on posterior margin (Figure 17; Pietsch 1974a:78, fig. 98); length of lower fork of operculum 26.6-27.7% of SL; ratio of lengths of upper and lower forks of operculum 0.47-0.51.

Epibranchial teeth absent; teeth present on pharyngobranchial II.

Counts and measurements in Table 5.

Distribution.—All five known specimens of *O. schmidti*, including the holotype, were collected in the Banda Sea.

Oneirodes micronema Grobecker 1978, Figure 18.

Material.—LACM 36039-3, 89 mm SL, stn 113 (holotype); LACM 36043-3, 17 mm SL, stn 157 (paratype).

This species, a member of the *O. schmidti* group (Pietsch 1974a), was recently described by Grobecker (1978) based on two females collected in the Banda Sea.

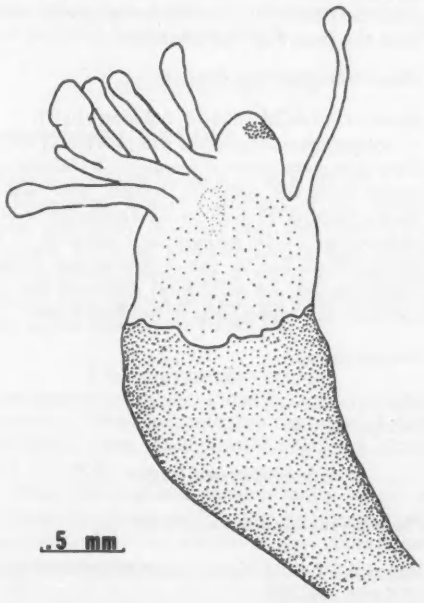


FIGURE 18.—Esca of *Oneirodes micronema*, holotype, LACM 36039-3, 89 mm SL, left lateral view.

Oneirodes sp. of *Oneirodes schmidti* Group, Bertelsen 1951

Material.—LACM 36046-6, metamorphosed female, 13 mm SK, stn 97 (illicium length 36.9% of SL).

Oneirodes sp.

Material.—Adolescent and adult males and females, and metamorphosing stages not identifiable to species or species group. Metamorphosed females representing possible new species: LACM 36087-5, 13 mm SL, stn 135 (illicium 15.4% of SL, upper jaw teeth 14, lower jaw teeth 21, pectoral fin rays 15); LACM 36089-5, 14 mm SL, stn 137 (illicium 14.3% of SL, upper jaw teeth 15, lower jaw teeth 20, pectoral fin rays 15; esca like that of LACM 36087-5); LACM 36115-2, 21 mm SL, stn 102 (illicium 23.8% of SL, upper jaw teeth 27, lower jaw teeth 38, pectoral fin rays 16). Metamorphosing females: LACM 36121-1, 2(7.5-9 mm SL), stn 178; LACM 36106-2, 8.5 mm SL, stn 187; LACM 36088-3, 9.5 mm SL, stn 136; LACM 36049-3, 9.5 mm SL, stn 194; LACM 36073-3, 10 mm SL, stn 94; LACM 36087-3, 10 mm SL, stn 135; LACM 36028-4, 10 mm SL, stn 141; LACM

36046-5, 11 mm SL, stn 97; LACM 36027-3, 11 mm SL, stn 147; LACM 36076-4, 11.5 mm SL, stn 26. Metamorphosed males: LACM 36108-2, 8.5 mm SL, stn 192; LACM 36087-2, 4(9-10 mm SL), stn 135; LACM 36081-2, 3(9.5 mm SL), stn 127a; LACM 36104-2, 2(9.5-11.5 mm SL), stn 175; LACM 36039-5, 2(10-11 mm SL), stn 113; LACM 36024-4, 3(10-12 mm SL), stn 81; LACM 36057-5, 2(10-12 mm SL), stn 93; LACM 36023-4, 4(10-12 mm SL), stn 143; LACM 36028-3, 3(10-13.5 mm SL), stn 141; LACM 36048-4, 10.5 mm SL, stn 36; LACM 36073-5, 2(10-5 mm SL), stn 94; LACM 36117-2, 10.5 mm SL, stn 173; LACM 36109-4, 10.5 mm SL, stn 193; LACM 36119-1, 2(10.5-13.5 mm SL), stn 96; LACM 36026-2, 11 mm SL, stn 122; LACM 36090-2, 3(11-12 mm SL), stn 138; LACM 36027-3, 11 mm SL, stn 147; LACM 36118-2, 11 mm SL, stn 180; LACM 36076-6, 12 mm SL, stn 26; LACM 36095-2, 12 mm SL, stn 149; LACM 36077-4, 12 mm SL, stn 155; LACM 36122-1, 12 mm SL, stn 179; LACM 36084-2, 2(12-12.5 mm SL), stn 130; LACM 36091-3, 2(12-12.5 mm SL), stn 142; LACM 36089-3, 6(12-13 mm SL), stn 137; LACM 36085-2, 3(12-14 mm SL), stn 133; LACM 36120-1, 12.5 mm SL, stn 123; LACM 36041-4, 4(12.5-13 mm SL), stn 39; LACM 36088-2, 13 mm SL, stn 136; LACM 36024-3, 13 mm SL, stn 81.

Danaphryne Bertelsen 1951

Danaphryne nigrifilis (Regan and Trewavas 1932)

Danaphryne nigrifilis is known from eight specimens, one of which (the holotype, 24 mm SL, ZMUC P92102) was collected by the *Dana* in the South China Sea (Bertelsen and Pietsch 1977). No additional material was provided by the *Alpha Helix*.

Microlophichthys Regan and Trewavas 1932

Microlophichthys microlophus (Regan 1925)

Material.—LACM 36024-7, male, 17 mm SL, stn 81; LACM 36048-3, female, 22 mm SL, stn 36; LACM 36047-3, female 29 mm SL, stn 89.

Twenty-three metamorphosed females of this species (12-99 mm SL) have been previously reported from localities in the Atlantic, Indian, and Pacific Oceans (Bertelsen and Pietsch 1977). Two additional females and a male were collected by the *Alpha Helix* in the Banda and Ceram Seas. In all respects, these specimens fall within the observed variation of *M. microlophus*.

Chirophryne Regan and Trewavas

Chirophryne xenolophus Regan and Trewavas 1932

Chirophryne xenolophus is known from only two specimens, the holotype (11 mm SL, ZMUC P9296) collected by the *Dana* in the South China Sea, and a second specimen (22 mm SL, SIO 70-306) from off Japan at about lat. 32°10′ N, long. 136°05′ E (Pietsch 1978).

Dolopichthys Garman 1899

Dolopichthys pullatus Regan and Trewavas 1932

Material.—LACM 36116-2, 113 mm SL, stn 84.

Thirty-three metamorphosed females of *D. pullatus* (10-115 mm) have been previously reported from localities in the Atlantic, the Gulf of Mexico, and the eastern Pacific and Indian Oceans (Pietsch 1972). The holotype of *D. pullatus* is the only previous record from the western Pacific. One additional specimen collected by the *Alpha Helix* from the Banda Sea constitutes the second record from the Indo-West Pacific Ocean.

Dolopichthys longicornis Parr 1927

Material.—LACM 36046-3, 8.5 mm, stn 97.

Dolopichthys longicornis was previously known from 18 metamorphosed females (14-159 mm) collected from the Atlantic, Indian, and eastern Pacific Oceans (Pietsch 1972). The holotype of *D. mucronatus* (= *D. longicornis*), collected in the South China Sea, is the only previous western Pacific record. An additional specimen was collected by the *Alpha Helix* in the Banda Sea.

Dolopichthys sp.

Material.—LACM 36071-2, metamorphosed male, 12 mm, stn 59.

Chaenophryne Regan 1925

Chaenophryne longiceps Regan 1925

Material.—LACM 36039-4, metamorphosed male, 10.5 mm, stn 113.

This species has a cosmopolitan distribution in all three major oceans of the world (Pietsch 1975).

A single male taken by the *Alpha Helix* in the Banda Sea consitutes the second record for this species in southeast Asian waters.

Chaenophryne draco Beebe 1932

Material.—LACM 36073-6, 17 mm, stn 94; LACM 36123-1, 21.5 mm, stn 80.

Chaenophryne draco has a wide distribution occurring in all three major oceans of the world (Pietsch 1975). Two metamorphosed females collected by the *Alpha Helix* in the Banda Sea constitute the first records of this species in southeast Asian waters.

Chaenophryne sp. of *Chaenophryne draco* Group

Material.—LACM 36046-7, metamorphosed male, 10 mm, stn 97.

Pentherichthys Regan and Trewavas

Pentherichthys sp.

The genus *Pentherichthys* is represented in southeast Asian waters by only two larval specimens (Bertelsen 1951). No additional material was provided by the *Alpha Helix*.

Lophodolos Lloyd 1909

Lophodolos indicus Lloyd 1909

Material.—LACM 36116-4, 69 mm, stn 84.

Twenty-two female specimens of this species were previously recorded from localities in the eastern Atlantic, and the Indian and Pacific Oceans between about lat. 4° S and 30° N (Pietsch 1974b). One additional specimen was collected by the *Alpha Helix* in the Banda Sea.

Oneirodidae gen. et sp.?

Material.—Two metamorphosing males: LACM 36069-3, 11 mm, stn 28; LACM 36039-3, 11.5 mm, stn 113.

These two metamorphosing males cannot be reasonably placed within any known oneirodid genus. Both are very similar in having the following characteristics:

Description.—Nostrils opening forward; skin between anterior nostrils lightly pigmented; posterior nostril well separated from eye; operculum deeply notched posteriorly; suboperculum short and broad, upper end rounded; inner side of suboperculum darkly pigmented; subdermal pigment continuous over body to posterior margin of caudal peduncle; pectoral rays on end of a relatively short, broad lobe; dorsal fin rays 6, anal fin rays 4, pectoral fin rays 15.

Comments.—These males are similar to *Oneirodes* and *Microlophichthys* in having a short, rounded suboperculum. They differ from *Oneirodes*, however, in having the skin between the anterior nostrils lightly pigmented, the inner surface of the suboperculum darkly pigmented, and the body covered with subdermal pigment to the base of the caudal fin. On the other hand, they differ from *Microlophichthys* in the absence of a distinct, separate patch of pigment on the caudal peduncle, and in having four, instead of five anal fin rays.

THAUMATICHTHYIDAE

Thaumatichthys Smith and Radcliffe 1912

Thaumatichthys pagidostomus Smith and Radcliffe 1912

Thaumatichthys pagidostomus is known from only the holotype (60 mm SL, USNM 72952) collected by the *Albatross* off Sulawesi (Bertelsen and Struhsaker 1977).

CENTROPHRYNIDAE

Centrophryne Regan and Trewavas 1932

Centrophryne spinulosa Regan and Trewavas 1932

Centrophryne spinulosa is known from 15 metamorphosed females and 2 metamorphosing males. The lectotype (39 mm SL female, ZMUC P92122), collected by the *Dana* off the northern coast of New Guinea, is the only record from the western Pacific (Pietsch 1972).

CERATIIDAE

Key to Females of Genera and Species of Ceratiidae

1A. Illicium long, much longer than bulb

of esca; 2 caruncles on back; subopercle without spine on anterior margin .... *Ceratias* sp.

1B. Illicium short, nearly completely enveloped by bulb of esca; 3 caruncles on back; subopercle with spine on anterior margin ..... *Cryptopsaras couesi* Gill

Ceratias Kröyer 1845

Ceratias sp.

Material.—LACM 36046-9, 9 mm, stn 97; LACM 36034-3, 2(10-18 mm), stn 85; LACM 36047-4, 10.5 mm, stn 89; LACM 36073-7, 11 mm, stn 94; LACM 36125-1, 12 mm, stn 72; LACM 36032-5, 13 mm, stn 110; LACM 36074-4 13.5 mm, stn 120; LACM 36076-7, 13.5 mm, stn 26; LACM 36027-4, 15 mm, stn 147; LACM 36064-2, 16.5 mm, stn 152; LACM 36058-2, 18 mm, stn 99; LACM 36029-2, 23 mm, stn 162; LACM 36093-2, 25 mm, stn 146.

Fourteen female specimens of the genus *Ceratias* were collected by the *Alpha Helix* from the Banda, Celebes, Ceram, and Halmahera Seas. All of these are adolescent females in which the diagnostic characters of the esca have not as yet developed. Since there are two, perhaps three species of *Ceratias* (Bertelsen 1951), specific identification is impossible at this time.

Cryptopsaras Gill 1883

Cryptopsaras couesi Gill 1883

Material.—LACM 36031-4, 8 mm, stn 58; LACM 36090-3, 3(8.5-12.5 mm), stn 138; LACM 36029-3, 2(9.5-10 mm), stn 162; LACM 36042-2, 10 mm, stn 74; LACM 36074-5, 10 mm, stn 120; LACM 36034-4, 10 mm, stn 85; LACM 36100-3, 10 mm, stn 166; LACM 36109-5, 10 mm, stn 193; LACM 36087-8, 2(10-10.5 mm), stn 135; LACM 36040-4, 3(10-102 mm), stn 27; LACM 36051-4, 11 mm, stn 38; LACM 36028-6, 11 mm, stn 141; LACM 36129-1, 11 mm, stn 181; LACM 36130-1, 11 mm, stn 186; LACM 36085-4, 2(11-13 mm), stn 133; LACM 36089-6, 11.5 mm, stn 137; LACM 36063-3, 11.5 mm, stn 140; LACM 36077-5, 2(11.5-12.5 mm), stn 155; LACM 36127-1, 12 mm, stn 167; LACM 36122-3, 12 mm, stn 179; LACM 36126-1, 12.5 mm, stn 18; LACM 36037-2, 12.5 mm, stn 82; LACM 36117-3, 12.5 mm, stn 173; LACM 36084-3, 6(12.5-85 mm), stn 130; LACM 36055-2, 13 mm, stn 79; LACM 36091-5, 13 mm, stn 142; LACM 36108-3, 13 mm, stn 192; LACM 36067-4, 14 mm, stn 23; LACM 36075-5, 14 mm, stn 121; LACM 36064-3, 4(14-19.5 mm), stn 152; LACM 36080-2, 16 mm, stn 126; LACM 36128-1, 19.5 mm, stn 91; LACM 36073-8, 59 mm, stn 94; LACM 36124-2, 94 mm, stn 112.

Cryptopsaras couesi has a cosmopolitan distribution in all three major oceans of the world (Bertelsen 1951). Fifty specimens were collected by the *Alpha Helix* from the Banda, Celebes, Halmahera, Sulu, and Timor Seas.

GIGANTACTINIDAE

Gigantactis Brauer 1902

Gigantactis vanhoeffeni Brauer 1902

Material.—LACM 36031-1, 17 mm, stn 58; LACM 36039-6, 2(24-31 mm), stn 113; LACM 36032-1, 25 mm, stn 110; LACM 36046-10, 26 mm, stn 97; LACM 36131-1, 32 mm, stn 51; LACM 36034-5, 34 mm, stn 85.

The *Alpha Helix* collected seven females (six metamorphosed and one in metamorphosis) of *G. vanhoeffeni*, all from the Banda Sea. These have been incorporated in a forthcoming revision of the Gigantactindae (Bertelsen et al. in press).

Gigantactis sp. Male Group II, Bertelsen et al. in press

Material.—LACM 36034-1, 2(12-12.5 mm), stn 85; LACM 36033-1, 2(13-14 mm), stn 88; LACM 36032-1, 13.5 mm, stn 110.

Gigantactis sp. Male Group IV, Bertelsen et al. in press

Material.—LACM 36030-1, 16.5 mm, stn 109.

Gigantactinidae gen. et sp.?

Material.—LACM 36024-6, male, 11.5 mm, stn 81.

This male cannot reasonably be placed within either of the two known gigantactinid genera (Bertelsen et al. in press).

LINOPHRYNIDAE

Key to Females of Genera and Species of Southeast Asian Linophrynidae

1A. Skin transparent; hyoid barbel absent;

jaw teeth small and numerous .... *Edriolychnus schmidti* Regan

1B. Skin darkly pigmented; hyoid barbel present; teeth large and few .... *Linophryne* Collett.. 2

2A. Distal escal appendages present; barbel distally divided into about 6 branches .. .. *Linophryne corymbifera* Regan and Trewavas

2B. Distal escal appendages absent; barbel unbranched .... *Linophryne trewavasae* Bertelsen

Edriolychnus Regan 1925

Edriolychnus schmidti Regan 1925

Edriolychnus schmidti is a relatively common ceratioid occurring in all three major oceans of the world (Bertelsen 1951). No additional material, however, was provided by the *Alpha Helix* in 1975.

Linophryne Collett 1886

Linophryne corymbifera Regan and Trewavas 1932

Material.—LACM 36046-11, female, 42 mm SL with parasitic male, 9.5 mm SL, stn 97.

A single female with parasitic male, representing the first known incidence of sexual parasitism in this species, was collected by the *Alpha Helix* in the Banda Sea. The specimen was referred to as *Linophryne* sp. A by Hansen and Herring (1977), and recently described and figured by Bertelsen (1978).

Linophryne trewavasae Bertelsen 1978

Material.—LACM 36116-5, female, 73.5 mm SL with parasitic male, 10.7 mm SL, stn 84 (holotype).

Linophryne trewavasae was recently described by Bertelsen (1978) from a single female with an attached male collected by the *Alpha Helix* in the Banda Sea. The specimen was referred to as *Linophryne* sp. B by Hansen and Herring (1977).

Linophryne sp. male

Material.—LACM 36088-5, a male, 15 mm SL, stn 136.

This single male specimen could not be identified to species.

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APPENDIX TABLE 1.—*Alpha Helix* stations that yielded Ceratioidei during the Southeast Asian Bioluminescence Expedition of 1975. Coordinates are for starting position only.

Station	Sea	Latitude	Longitude	Gear depth(m)	Time (h)	Date
18	Timor	8°49.8′ S	129°43.0′ E	0-550	0900-1400	20 March
23	Banda	4°39.2′ S	129°54.1′ E	0-2,000	2225-0530	26 March
24	Banda	4°39.1′ S	129°53.7′ E	0-2,000	0115-0745	28 March
25	Banda	4°16.8′ S	129°34.4′ E	0-1,800	2010-0340	28 March
26	Ceram	2°46.0′ S	127°53.7′ E	0-1,500	0150-0800	31 March
27	Ceram	2°45.3′ S	127°55.1′ E	0-2,000	0150-0800	1 April
28	Ceram	3°14.8′ S	127°38.0′ E	0-100	2035-2205	1 April
36	Banda	4°54.0′ S	129°30.5′ E	830-1,050	1440-1620	11 April
37	Banda	4°56.3′ S	129°25.5′ E	0-2,000	1900-0155	11 April
38	Banda	4°40.4′ S	129°39.0′ E	0-780	0320-0530	12 April
39	Banda	4°45.6′ S	129°51.2′ E	0-1,000	0950-1435	13 April
51	Banda	4°56.2′ S	129°50.0′ E	550-815	1545-1655	14 April
58	Banda	4°54.5′ S	129°48.4′ E	650-810	1200-1400	16 April
59	Banda	4°57.3′ S	129°44.0′ E	1,100-1,300	1555-1755	16 April
66	Banda	4°54.0′ S	129°47.5′ E	1,500-2,000	1515-1815	17 April
71	Banda	4°55.5′ S	129°39.0′ E	1,500-2,000	1048-1523	19 April
72	Banda	4°48.5′ S	129°58.0′ E	0-600	1645-1905	19 April
74	Banda	5°04.0′ S	129°54.5′ E	720-990	0041-0241	19 April
79	Banda	4°57.5′ S	129°51.0′ E	0-710	1845-2200	27 April
80	Banda	4°48.7′ S	129°47.2′ E	0-710	2314-0220	28 April
81	Banda	4°56.5′ S	129°59.5′ E	1,000-1,500	0416-0616	28 April
82	Banda	5°02.8′ S	130°07.0′ E	0-690	0745-1050	28 April
84	Banda	5°04.5′ S	130°12.0′ E	0-1,500	1400-2100	28 April
85	Banda	4°57.5′ S	130°11.7′ E	0-750	2115-0025	28 April
87	Banda	4°52.0′ S	129°50.0′ E	0-870	0915-1215	1 May
88	Banda	4°58.0′ S	129°43.0′ E	1,000-1,500	1450-1650	1 May
89	Banda	5°03.5′ S	129°41.0′ E	0-960	1820-2112	1 May
91	Banda	4°55.0′ S	130°00.0′ E	0-600	1030-1250	5 May
93	Banda	5°02.3′ S	130°19.5′ E	0-760	1650-2013	5 May
94	Banda	5°01.5′ S	130°04.6′ E	650-1,000	2245-0045	5 May
96	Banda	5°00.0′ S	129°54.0′ E	0-300	0520-0615	6 May
97	Banda	4°54.0′ S	129°42.7′ E	0-850	0700-1025	6 May
99	Banda	5°03.0′ S	129°52.0′ E	0-460	2020-2242	6 May
102	Banda	4°45.0′ S	129°19.7′ E	0-2,000	0540-1045	7 May
103	Banda	4°49.0′ S	129°31.0′ E	550-940	1415-1630	7 May
109	Banda	4°33.0′ S	129°17.0′ E	0-1,100	0030-0445	12 May
110	Banda	4°47.4′ S	129°51.8′ E	0-1,500	0945-1235	13 May
112	Banda	4°58.0′ S	129°59.5′ E	650-850	1745-1855	13 May
113	Banda	5°07.5′ S	130°08.4′ E	650-1,000	2120-2255	13 May
120	Halmahera	0°32.0′ S	129°08.3′ E	450-1,100	1125-1325	16 May
121	Halmahera	0°41.7′ S	128°55.7′ E	1,000-1,400	1730-1930	16 May
122	Halmahera	0°36.3′ S	129°03.2′ E	575-600	2240-2340	16 May
123	Halmahera	0°29.7′ S	129°02.7′ E	1,000-1,050	0205-0410	17 May
126	Halmahera	0°22.1′ S	129°01.3′ E	450-600	1042-1142	17 May
127a	Halmahera	0°04.5′ S	128°26.5′ E	0-750	1820-2155	17 May
130	Halmahera	0°06.0′ S	128°28.7′ E	600-790	0724-0933	18 May
133	Halmahera	0°05.7′ N	128°24.8′ E	0-680	1520-1833	18 May
135	Halmahera	0°06.2′ S	128°38.3′ E	820-1,000	2306-0106	18 May
136	Halmahera	0°17.4′ S	128°47.5′ E	1,000-1,250	0446-0646	19 May
137	Halmahera	0°08.9′ S	128°40.0′ E	0-960	0955-1300	19 May
138	Halmahera	0°05.1′ N	128°29.0′ E	750-900	2150-2250	19 May
140	Halmahera	0°00.6′ S	128°46.3′ E	250-320	0202-0310	20 May
141	Halmahera	0°05.0′ S	128°52.7′ E	1,000-1,100	0625-0855	20 May
142	Halmahera	0°10.5′ S	128°33.3′ E	750-1,000	1200-1400	20 May
143	Halmahera	0°14.5′ S	128°46.7′ E	1,250-1,500	1715-1930	20 May
146	Halmahera	0°36.2′ S	129°12.0′ E	420-600	0437-0537	21 May
147	Halmahera	0°40.0′ S	128°58.5′ E	0-1,200	0635-0935	21 May
149	Halmahera	0°22.5′ S	128°57.8′ E	420-600	1640-1740	21 May
150	Halmahera	0°18.5′ S	129°00.8′ E	700-1,000	2003-2203	21 May
152	Halmahera	0°13.0′ S	129°06.5′ E	180-300	0145-0345	22 May
155	Halmahera	0°38.6′ S	129°05.6′ E	680-850	1210-1400	22 May
157	Banda	4°09.6′ S	130°50.0′ E	0-840	0215-0615	24 May
162	Celebes	2°37.6′ N	124°46.5′ E	550-800	0917-1117	1 June
166	Sulu	7°10.7′ N	121°25.6′ E	660-800	0712-0900	3 June
167	Sulu	7°19.2′ N	121°20.1′ E	950-1,100	1210-1410	3 June
173	Sulu	8°06.3′ N	121°13.2′ E	730-810	0645-0845	4 June
175	Sulu	8°28.3′ N	121°15.0′ E	920-1,100	1422-1622	4 June
178	Sulu	8°47.0′ N	121°26.0′ E	790-910	0200-0330	5 June
179	Sulu	8°58.5′ N	121°42.2′ E	1,500-2,000	0605-1005	5 June
180	Sulu	9°06.0′ N	121°51.0′ E	710-790	1340-1550	5 June
181	Sulu	9°16.8′ N	122°02.2′ E	820-950	1905-2105	5 June
183	Sulu	9°24.5′ N	122°12.3′ E	890-890	0115-0215	6 June
184	Sulu	9°18.0′ N	122°10.0′ E	480-550	0355-0455	6 June
186	Sulu	9°03.7′ N	122°03.6′ E	360-640	0936-1036	6 June
187	Sulu	8°53.0′ N	122°01.5′ E	830-900	1255-1455	6 June
192	Sulu	9°08.0′ N	122°02.5′ E	800-900	0500-0700	7 June
193	Sulu	9°21.5′ N	122°14.7′ E	800-1,100	1020-1240	7 June
194	Sulu	9°28.3′ N	122°06.8′ E	0-1,500	1350-1740	7 June

EGGS AND LARVAE OF BUTTER SOLE, *ISOPSETTA ISOLEPIS* (PLEURONECTIDAE), OFF OREGON AND WASHINGTON

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ABSTRACT

Development of butter sole, *Isopsetta isolepis*, is described from egg through benthic juvenile, based on reared and field-collected specimens.

Isopsetta isolepis eggs are planktonic, spherical, and transparent with a narrow perivitelline space, homogeneous yolk, and no oil globule. Diameters of 80 reared eggs averaged 0.93 mm (range 0.90-0.99 mm). Using light microscopy, early and middle stage eggs are indistinguishable from those of three other pleuronectids, English sole, *Parophrys vetulus*, sand sole, *Psettichthys melanostictus*, and starry flounder, *Platichthys stellatus*, with which they cooccur. Pigment patterns distinguish late stage *I. isolepis* eggs from those of *Psettichthys melanostictus* and *Platichthys stellatus*. Because the late stages of *I. isolepis* embryos vary widely in degree and character of pigmentation, they often cannot be reliably separated from those of *Parophrys vetulus*.

Larvae are readily distinguished by three bands of melanistic pigment on the tail region of the body combined with myomere counts (39-42). Transformation from larva to juvenile takes place at about 18-23 mm. Larvae are abundant in nearshore coastal waters off Oregon and Washington in winter and spring, where they cooccur with larvae of *P. vetulus*. Recently transformed benthic juveniles of *I. isolepis* usually are found offshore rather than in the bay and nearshore habitats occupied by young juvenile *P. vetulus*.

This paper presents the first complete description of development of the butter sole, *Isopsetta isolepis* (Lockington), from egg through benthic juvenile. Larvae of this species are common in the ichthyoplankton off Oregon and Washington where they ranked fifth in overall abundance in April and May 1967 (Waldron 1972) and third in a coastal assemblage of larval fishes off Oregon in 1971-72 (Richardson and Pearcy 1977; Richardson[4]).

Isopsetta, a monotypic genus of the family Pleuronectidae, ranges from Ventura, Calif., to the Bering Sea (Miller and Lea 1972). It is usually found in coastal waters although it has been reported from the 274-366 m depth zone in western Alaska (Demory 1971; Miller and Lea 1972; Hart 1973). Adult butter sole ranked 11th and 7th in biomass of all flatfishes taken during trawl surveys off Oregon in 1971-72 and 1973-74 (Demory et al.[5]) and 6th in biomass of all flatfishes off Washington in both 1975 and 1976 (Barss et al.[6]). Because it is a relatively small, <55 cm TL (total length), slender fish (Miller and Lea 1972; Hart 1973), it is currently of only minor commercial importance.

Levings (1968) briefly described *I. isolepis* eggs as single, nonadhesive, transparent, spherical, without an oil globule, with a mean egg diameter of 1.013 mm, although he did not illustrate them. The eggs sank at salinities ≤26.61‰ but floated at salinities ≥28.03‰. Levings concluded that the eggs were demersal within Skidegate Inlet, British Columbia, where bottom salinities were 24.96‰. *Isopsetta isolepis* larvae 4.8, 7.9, 10.0, and 15.5 mm long from Puget Sound were sketched by Blackburn (1973) but were labeled *Lyopsetta exilis*. He also provided short descriptions.

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[4]Richardson, S. L. 1977. Larval fishes in ocean waters off Yaquina Bay, Oregon: abundance, distribution, and seasonality, January 1971 to August 1972. Oreg. State Univ., Sea Grant Coll. Prog., Publ. ORESU-T-77-003, 73 p.

[5]Demory, R. L., M. J. Hosie, N. TenEyck, B. O. Forsberg. 1976. Marine resource surveys on the continental shelf off Oregon, 1971-74. Oreg. Dep. Fish Wildl., Completion Rep., June 1976, 49 p.

[6]Barss, W. H., R. L. Demory, N. TenEyck. 1977. Marine resource surveys on the continental shelf and upper slope off Washington, 1975-76. Oreg. Dep. Fish Wildl., Completion Rep., September 1977, 34 p.

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METHODS

Eggs from ripe fish collected in Bellingham Bay, Wash., were artificially fertilized on 12 March 1974 and were reared at the Mukilteo field station of the Northwest and Alaska Fisheries Center (NWAFC), National Marine Fisheries Service (NMFS), NOAA, Seattle, Wash. The eggs were incubated in 0.6 or 1.0 l glass beakers containing local Puget Sound seawater maintained at 9°-10° C. Subsamples of eggs were preserved in Formalin[7] in eight time periods, 4, 9, 20, 24, 48, 72, 96, and 120 h, after fertilization. Subsamples of larvae were preserved for each of 13 time periods: at hatching (144 h or 6 d after fertilization) and at 2, 3, 4, 7, 9, 11, 14, 16, 18, 21, 23, and 25 d after hatching. Although rotifers (*Brachionus plicatilus*) were added to the containers at various levels (4, 8, and 16 rotifers/ml seawater), the larvae did not feed actively and all were dead by 22 April 1974.

Approximately 300 larvae were obtained from NWAFC collections made off coastal Washington in 1972. An additional 107 larvae were obtained from Oregon State University (OSU) ichthyoplankton collections taken off the Oregon coast from 1971 to 1972 (Richardson and Pearcy 1977; Richardson see footnote 4). Benthic juveniles were collected in beam trawls off the mouth of the Columbia River in June and September 1975 (Richardson et al.[8]).

Counts of meristic structures were made on 209 larvae (3.2-23.6 mm) and 7 juveniles (44-160 mm) taken from the OSU and NWAFC collections. Larvae were stained with Alizarin Red S using Taylor's (1967) enzyme method to determine sequence of ossification. Some (45) were subsequently restained with Alcian Blue and Alizarin Red using techniques described by Dingerkus and Uhler (1977). Counts were made of dorsal fin rays, anal fin rays, caudal fin rays, left and right pectoral fin rays, branchiostegal rays, gill rakers, vertebral centra, neural spines, and haemal spines. Fin rays and vertebrae were counted even if they were tinted only slightly with alizarin stain. Uptake and retention of alizarin in ossified structures may vary depending upon the length of time the specimens have been in preservative. Differential loss of stain may account for some of the variation observed in the onset of ossification of certain structures such as teeth.

Measurements were made using an ocular micrometer in a stereomicroscope. The greatest outside diameter and greatest yolk diameter were recorded for 80 eggs from the reared series, 10 for each of the eight time periods that eggs were preserved from 4 to 120 h after fertilization. Measurements were made on 63 reared larvae, 5 specimens (when available) from each of the 13 time periods after hatching (6 d after fertilization) that larvae were preserved to 25 d after hatching. Size range of reared specimens was 2.7-5.3 mm SL (standard length). Measurements also were made on 107 larvae from plankton collections including 5 specimens (when available) for each 1.0 mm size class interval from 2 to 23 mm SL (range 2.9-23.6 mm). Body measurements were made on larvae as follows:

Standard length – snout tip to notochord tip until notochord is fully flexed and the posterior margin of the forming hypural elements is vertical, then to posterior margin of hypurals.

Head length – snout tip to cleithrum.

Body depth at pectoral fin base – vertical distance from dorsal body margin to ventral body margin, excluding finfold or fins, at the pectoral fin base.

Body depth at anus – vertical distance from dorsal body margin, excluding finfold or fin, to anus.

Body depth behind anus – vertical distance from dorsal body margin to ventral body margin, excluding finfolds or fins, at point immediately behind anus where body depth decreases greatly compared to depth at anus.

Body depth at caudal peduncle – before formation of caudal fin, vertical distance from dorsal body margin to ventral body margin, excluding finfolds or fins, at the posteriormost myomere; after caudal fin formation, least depth of caudal peduncle.

Snout length – snout tip to anterior margin of right eye.

Eye diameter – horizontal distance across right eyeball.

Snout to anus length – distance along body midline from snout tip to vertical through posterior margin of anus.

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[8]Richardson, M. D., A. G. Carey, Jr., W. A. Colgate. 1977. The effects of dredged material disposal on benthic assemblages off the mouth of the Columbia River. Final Rep., Dep. Army Corps Eng. Contracts DACW 57-75-C-0137 and DACW 57-56-C-0092, Vicksburg, Miss., 411 p.

Upper jaw length – snout tip to posterior margin of maxillary.

Illustrations of eggs and larvae were made with the aid of a camera lucida. All specimens had been preserved in 5% Formalin. Illustrations of the caudal fin and skeletal structure were made from cleared and stained specimens.

VERIFICATION OF IDENTIFICATION

Reared eggs were fertilized from known parents, thus their identity was certain.

A series of larval specimens from plankton collections was linked together by pigment pattern. The left eye had begun to migrate in the largest specimens indicating that they were pleuronectids, the only right-eyed flatfishes occurring off Oregon and Washington. Positive identification was based on knowledge of early stages of all but one of the pleuronectids occurring in the area (Table 1) and on the following meristic characters for *I. isolepis* (Hart 1973; Ahlstrom[9]; this study):

Dorsal fin rays	= 78-92
Anal fin rays	= 58-69
Abdominal vertebrae	= 9-11, usually 10
Total vertebrae	= 39-42
Caudal fin rays	= 17-18, usually 18
Pectoral fin rays	= 11-13
Pelvic fin rays	= 6
Branchiostegal rays	= 7
Gill rakers	= 4-6 + 7-8

Additional confirmation was provided by larvae reared to yolk depletion, which were similar to the smallest specimens from the plankton samples.

DISTINGUISHING FEATURES

Early and middle stage eggs of *I. isolepis* are indistinguishable from those of English sole, *Parophrys vetulus*; starry flounder, *Platichthys stellatus*; and sand sole, *Psettichthys melanostictus*. Chorions of reared eggs are often noticeably striated, but this characteristic is not consistent among reared eggs and is rarely seen in eggs from the plankton. Thus, chorion sculpturing is not useful for identifying *I. isolepis* eggs.

[9]E. H. Ahlstrom, Senior Scientist, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, unpubl. data.

TABLE 1.—Pleuronectid flatfishes occurring off Oregon and Washington with references on early developmental stages.

Species	References
Atheresthes stomias	Pertseva-Ostroumova (1960, 1961)
Embassichthys bathybius	Richardson (in press)
Eopsetta jordani	Alderdice and Forrester (1971); Ahlstrom (unpubl. data); Richardson (in press)
Glyptocephalus zachirus	Ahlstrom and Moser (1975)
Hippoglossoides elassodon	Dekhnik (1959); Pertseva-Ostroumova (1961); Miller (1969); Alderdice and Forrester (1974) Forrester and Alderdice[1]
Hippoglossus stenolepis	Thompson and Van Cleve (1936); Pertseva-Ostroumova (1961)
Inopsetta ischyra	None
Isopsetta isolepis	Levings (1968); Blackburn (1973)
Lepidopsetta bilineata	Pertseva-Ostroumova (1961); Blackburn (1973); Richardson (in press)
Lyopsetta exilis	Blackburn (1973); Ahlstrom and Moser (1975)
Microstomus pacificus	Hagerman (1952); Ahlstrom and Moser (1975)
Parophrys vetulus	Budd (1940)[2]; Orsi (1968); Blackburn (1973); Ahlstrom and Moser (1975); Misitano (1976)
Platichthys stellatus	Orcutt (1950); Yusa (1957); Pertseva-Ostroumova (1961) as *Pleuronectes stellatus*
Pleuronichthys coenosus	Budd (1940) (as *P. decurrens*); Sumida et al. (1979)
Pleuronichthys decurrens	Budd (1940) (as *P. coenosus*); Sumida et al. (1979)
Psettichthys melanostictus	Hickman (1959); Sommani (1969)

[1]Forrester, C. R., and D. F. Alderdice. 1968. Preliminary observations on the embryonic development of the flathead sole (*Hippoglossoides elassodon*). Fish. Res. Board Can., Tech. Rep. 100, 20 p.
[2]The 6.3 mm larva is not *P. vetulus*.

Late stage eggs are readily distinguished from other northeast Pacific pleuronectids with similar size eggs by means of pigment. Embryos in late stage *P. melanostictus* eggs have scattered yolk-sac melanophores, and those of *Platichthys stellatus* have pigmented finfolds, while *I. isolepis* embryos lack pigment in both places. *Isopsetta isolepis* embryos are most similar to those of *Parophrys vetulus*. While *I. isolepis* embryos usually have several isolated ventral tail melanophores, their number is quite variable, ranging from none to many, whereas *P. vetulus* embryos have so many ventral tail melanophores that the pigment appears almost continuous. The head and anterior trunk pigment of *I. isolepis* is more dendritic and melanophores are less numerous than on *P. vetulus*. Despite these differences, variation in both ventral tail and trunk melanophores, especially in *I. isolepis*, is so great that late stage eggs of the two species cannot always be reliably separated.

Most sizes of *I. isolepis* larvae can be easily distinguished from other flatfish larvae off Oregon and Washington by their body form together with their striking pigment pattern, most notably the three bands of melanophores on the body posterior to the abdominal cavity. After notochord flexion the posteriormost band lines the base of the caudal fin, but the two other bands remain apparent through transformation to benthic juvenile. No

other flatfish larvae of similar form in the area have three such bands. The only other three-banded flatfish larva is deepsea sole, *Embassichthys bathybius*, but it hatches at about 9 mm, has over 60 myomeres, and a different elongate form (Richardson in press). The most similar appearing banded larval flatfish is the flathead sole, *Hippoglossoides elassodon*, which has four pigment bands.

Before the three pigment bands become obvious, i.e., in larvae <4 mm SL, larvae of *I. isolepis* are similar to those of *P. vetulus*. They usually are separable by the size and distribution of postanal ventral midline melanophores. Those of *I. isolepis* are small and appear more or less as a double row when viewed from the ventral surface; those of *P. vetulus* are enlarged and stellate and appear as a single row when viewed ventrally.

Newly transformed *I. isolepis* juveniles are also similar to *P. vetulus*. Before development of adult characters such as scales on the fins of *I. isolepis*, which will easily separate the two, *I. isolepis* can usually be distinguished by remnants of the larval pigment bands on the blind side. The number of gill rakers on the lower limb (Miller and Lea 1972) also will separate the two species (7-8 for *I. isolepis* and 10-13 for *P. vetulus*).

DEVELOPMENT OF EGGS (Figure 1)

Isopsetta isolepis eggs are spherical and transparent, with a narrow perivitelline space, a homogeneous yolk, and no oil globule. Although the eggs apparently sink at salinities ≤26.61‰ (Levings 1968), they are taken in our plankton samples, and live eggs floated in the rearing experiments (salinity ~26.9‰). Diameters of 80 reared eggs averaged 0.93 mm (0.90-0.99 mm), while yolk diameters averaged 0.76 mm (0.60-0.95 mm).

Embryonic development is typical of most teleosts with planktonic eggs. The stages of egg development we use correspond to the basic divisions of embryonic development used by Ahlstrom and Counts (1955), with detailed subdivisions of each stage (Naplin and Obenchain in press).

Pigmentation

Pigment first appears during the middle stage of embryonic development. At this time, distinct melanophores are scattered unevenly from the middle of the eyes posteriorly over the trunk. The

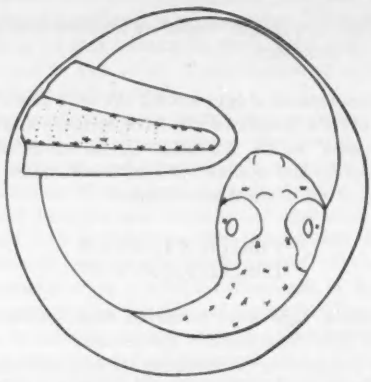

FIGURE 1.—*Isopsetta isolepis* eggs, late stage from plankton collections.

melanophores become more organized into two dorsolateral lines on the anterior somites, and diminish in size and frequency posteriorly. The dorsolateral lines are the site of melanophore formation, and pigment is present farther posteriorly as development continues.

The development of this species is unusual in that the anteriormost melanophores become increasingly dendritic and so fine that they gradually become less visible. By the time the embryos have reached the late stage (tail five-eighths of the way around the yolk), less head pigment is visible and the trunk is covered with very small but distinctly visible dendritic melanophores. Several distinct ventral melanophores lie at the juncture of the trunk and the yolk sac, and one or two isolated spots are on the yolk sac nearby. Most of the tail pigment is scattered dorsally in no obvious pattern, and several lateral melanophores are now in the ventral tail area.

When the tail is three-fourths of the way around the yolk, the head and trunk generally appear to be pigmented, although less distinctly than in the middle stage. Ventral trunk pigment is present, and some embryos may have one to three yolk-sac melanophores nearby. Scattered melanophores appear dorsally on the posterior trunk and on all surfaces of the tail. More lateral melanophores are present toward the tail tip.

From the time the tail is seven-eighths of the way around the yolk through hatching, little change in the pigment pattern occurs; however, the lateral tail melanophores have moved to become ventral. Dorsal and ventral tail pigment melanophores are

spread into thin lines between the margin of the body and finfold. The ventral melanophores are variable, ranging from no melanophores to many, and are separated at irregular intervals over the length of the tail, while the dorsal pigment can appear almost continuous. Near the tail tip the dorsal and ventral melanophores align, as in the early larvae, to form the precursor of the posteriormost band of pigment noted in the larvae.

The reared embryos appear more lightly pigmented than wild-caught embryos. In the latter, it is possible that the marked fading of the head pigment may not occur until after hatching.

Morphology

Physical development of *I. isolepis* embryos progresses as in other fishes. At the time of initial pigment formation, the blastopore has closed and the embryonic body is gradually thickening on top of the yolk sac. During this stage, the eyecups are forming, but no lens tissue is discernible. About 12 somites have formed, and Kupffer's vesicle is still visible just anterior to the tail bud.

When the tail is five-eighths of the way around the yolk, the eyecups are well-formed and lenses are present. The brain has differentiated into a forebrain and a larger midbrain. The auditory vesicles are forming but are not yet hollow. About 27 somites are present, Kupffer's vesicle is no longer visible, and the small tail has a definite finfold.

By the time the tail has reached three-fourths of the way around the yolk, the auditory vesicles are well-formed and immediately apparent. The embryo now has about 37 somites. Hatching can occur when the embryo's tail has reached seven-eighths of the way around the yolk to full circle. At this point, the embryo has the full complement of somites or myomeres (39-42) and is morphologically similar to a newly hatched larva.

DEVELOPMENT OF LARVAE (Figures 2-5)

Pigmentation

Pigment on newly hatched larvae is scattered lightly on the head and snout, and appears on the dorsal, lateral, and ventral body surface above the abdominal cavity and also in the tail region. No pattern is obvious. The eyes are unpigmented.

In the head region, the eyes begin to darken by 4 d (about 3.8-4.0 mm) after hatching and are fully pigmented by 7 d (3.9-4.1 mm) in the reared larvae. Eyes in the smallest plankton specimen (2.9 mm) are pigmented. During early development, pigment over the head and snout disappears (by about 4 mm in reared larvae, 2.9 mm in planktonic larvae) except for a few internal melanophores above the otic capsule. Pigment appears on the lower jar and throat region by 4 or 5 mm and persists through the larval period. By about 6 or 7 mm several melanophores are present at the ventral angle of the preopercle. Later in development, scattered melanophores are added on the head (>10 mm) and on the upper jaw (>14 mm). Additional pigment is added to the entire head region on the eyed side during transformation (>17 mm).

In the abdominal region, melanophores disappear from the dorsal and lateral body surfaces above the gut cavity by the time larvae are about 4 mm long. Pigment is added again in this region during the transformation period when larvae are about 17 mm long. It is added first in two patches on the dorsal pterygiophores. More melanophores are then added laterally as well as on the dorsal pterygiophores, mainly along the myosepta, obscuring the original patches. A series of internal melanophores develops dorsal to the notochord above the abdominal cavity in larvae >10 mm. Melanophores are added along the ventral margin of the gut cavity by the time larvae are about 4 mm long. With development, additional melanophores extend over the ventral and posterior portions of the abdominal cavity appearing in a half-moon shape on most larvae >8 mm long. This pattern persists until transformation when the increase in body pigment on the eyed side obscures it.

In the tail region, three characteristic bands of pigment become obvious in reared larvae 4 d (3.9-4.1 mm) after hatching and are visible on the 2.9 mm plankton caught larvae. These are located on the body at positions roughly 50, 67, and 90% SL. In larvae <10 mm, these bands generally extend from dorsal to ventral body margins. With development the middle band becomes the most pronounced of the three. This middle band remains visible on the eyed side of some newly transformed benthic juveniles, and remnants of it persist on the blind side of juveniles as long as 35 mm. After notochord flexion (>14 mm), the posterior band is seen as a line of pigment at the base of the caudal fin. The anterior band becomes less pronounced and often does not extend above the lateral midline in larvae >14 mm. Along the notochord, a series of internal melanophores develops dorsal to

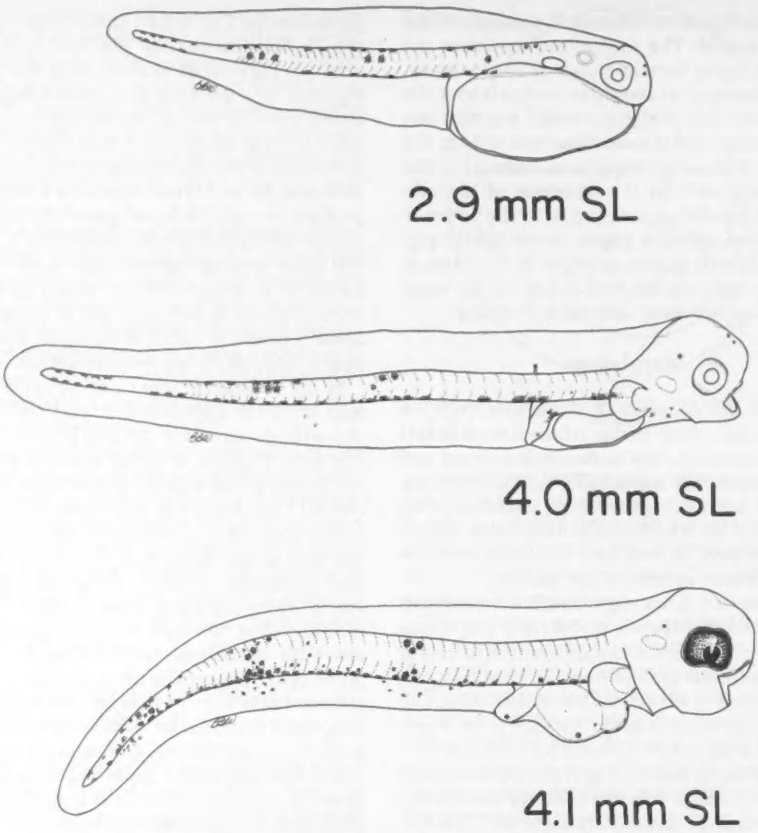

FIGURE 2.—*Isopsetta isolepis* larvae: 2.9 mm SL (reared, newly hatched, 144 h after fertilization); 4.0 mm SL (reared, 4 d after hatching); 4.1 mm SL (plankton specimen).

it, first in the region of the anterior two pigment bands in larvae about 6 or 7 mm long. Additional internal pigment spots then develop along the notochrod between the three pigment bands and anterior to them. This line of internal pigment spots is usually not continuous. It remains visible until the end of the transformation period. Along the ventral midline, pigment appears as a characteristic double row (viewed ventrally) of small melanophores in larvae >4 mm. This double row remains obvious until the onset of anal fin formation, about 14 mm, after which these melanophores appear to line the base of the anal fin, sometimes with one melanophore/fin ray. These melanophores become indistinct during transformation. On the ventrolateral body surface, melanophores are added just above the ventral midline row about the time the anal fin begins to form, around 10 mm. These melanophores eventually, by 12 mm, appear in the myosepta in a line midway between the lateral midline and the ventral margin of the body myomeres. Until the addition of pigment during transformation this line of melanophores is visible on the eyed side only, but is often visible on the blind side of newly transformed benthic juveniles. Along the margin of the ventral finfold a line of evenly spaced small melanophores is visible on newly preserved larvae >4 mm. This is often faded after a long period of preservation or is missing in plankton collected

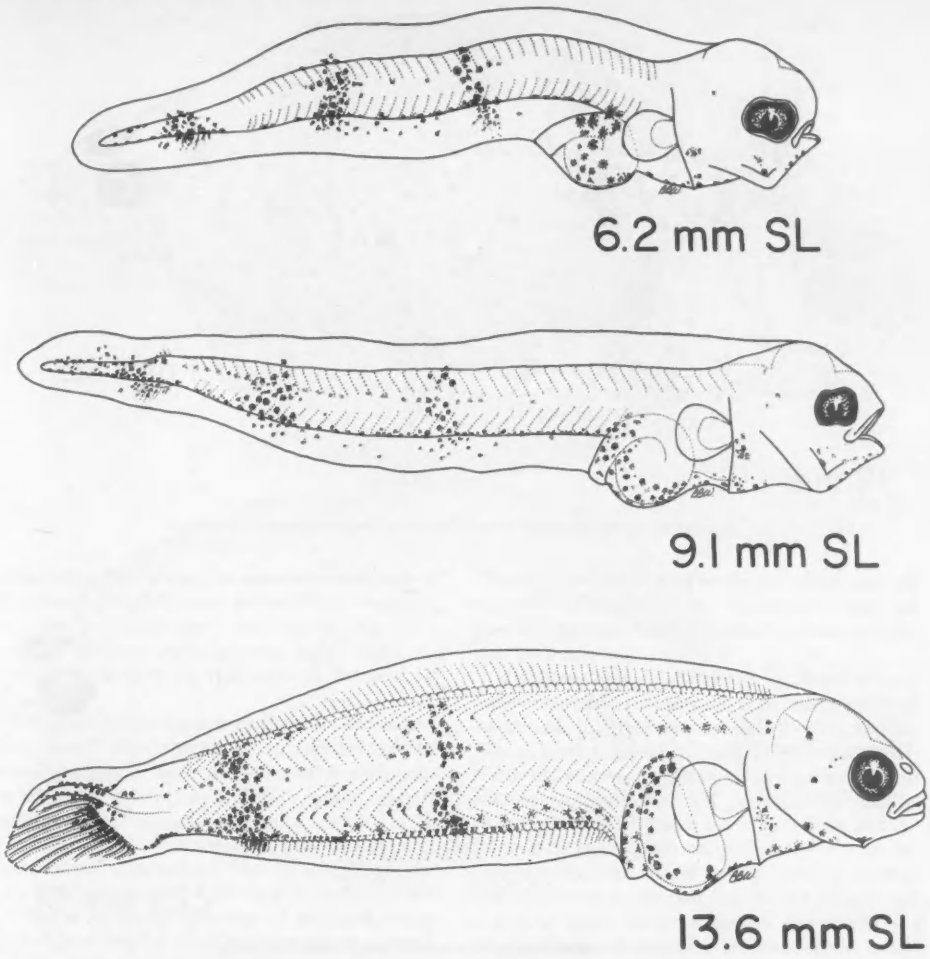

FIGURE 3.—*Isopsetta isolepis* larvae: 6.2 mm SL, 9.1 mm SL, and 13.6 mm SL.

specimens due to damaged finfolds. It is not visible on most specimens examined in this study, including the series illustrated. This line of melanophores has been seen on a few specimens up to 7.3 mm long. Additional pigment develops on the ventral finfold in the vicinity of the three pigment bands in larvae >4 mm and on the dorsal finfold near the posteriormost pigment band by the time larvae are 8 mm. This finfold pigment persists until caudal and anal fin formation. After the dorsal and anal fins are formed, by the time larvae are >15 mm, their margins are fringed with melanophores. However, the fin margins are often damaged on preserved planktonic specimens and the pigment fringing is not visible.

With transformation, at >17 mm, pigment is added to the eyed side in the tail region. Four or five clusters of melanophores appear along the dorsal pterygiophores and four along the ventral pterygiophores. These clusters eventually become obscured as more pigment is added. Increases in the number of melanophores along the bases of the

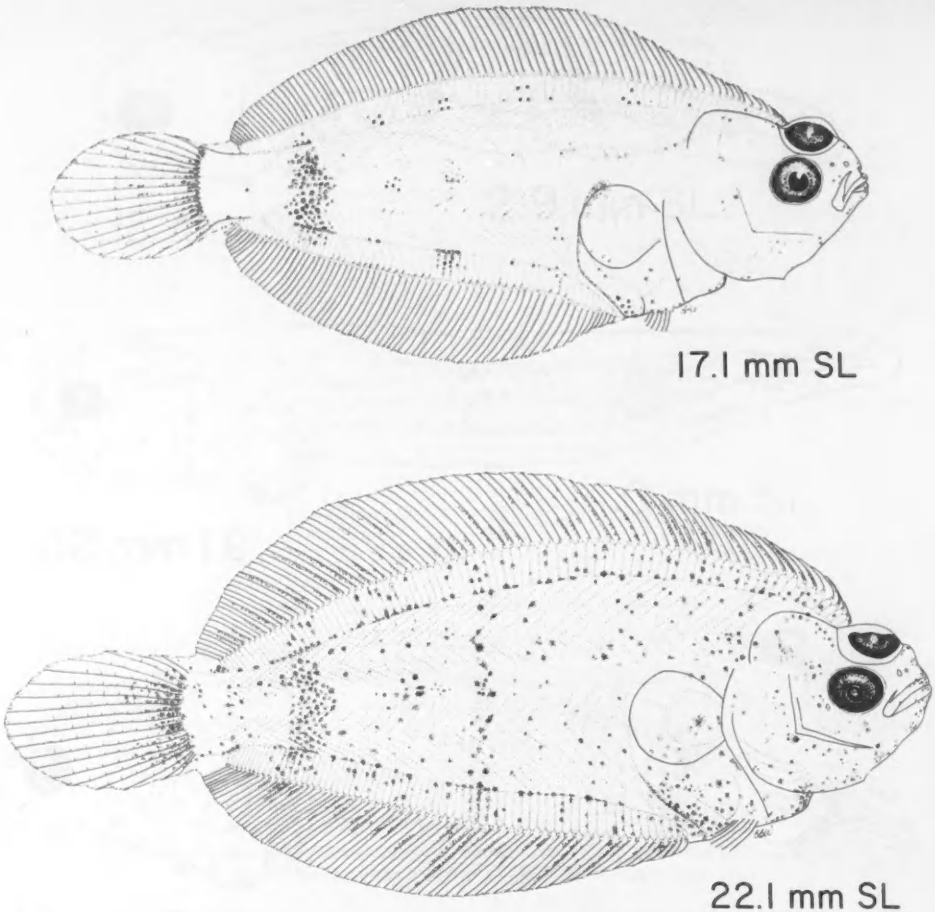

FIGURE 4.—*Isopsetta isolepis* larvae: 17.1 mm SL and 22.1 mm SL.

dorsal and anal pterygiophores give the appearance of solid lines of pigment. More melanophores appear on the body until all larval pigment is obscured. Additional pigment develops on the dorsal, anal, and caudal fins along the fin rays.

Morphology

Newly hatched reared larvae, 144 h after fertilization, range in length from 2.68 to 2.92 mm ($\bar{X}$ = 2.78 mm, based on 50 specimens). The yolk sac extends along the anterior third of the body. The mouth is not yet formed. A moderate finfold extends from the head around the posterior part of the body to the anus. The otic capsule is visible on the head behind the unpigmented eye. The mouth is formed by 2 d (3.4-3.5 mm) after hatching. The yolk is nearly gone by 4 d (3.8-4.0 mm) and is no longer visible by 7 d (3.9-4.1 mm). By 11 d (3.3-4.1 mm) the previously straight gut begins to coil. The smallest larva identified from plankton collections is 2.9 mm. It has a formed mouth, no remnant of yolk, and its gut has begun to coil. The size discrepancy may be an artifact of preservation, or it may

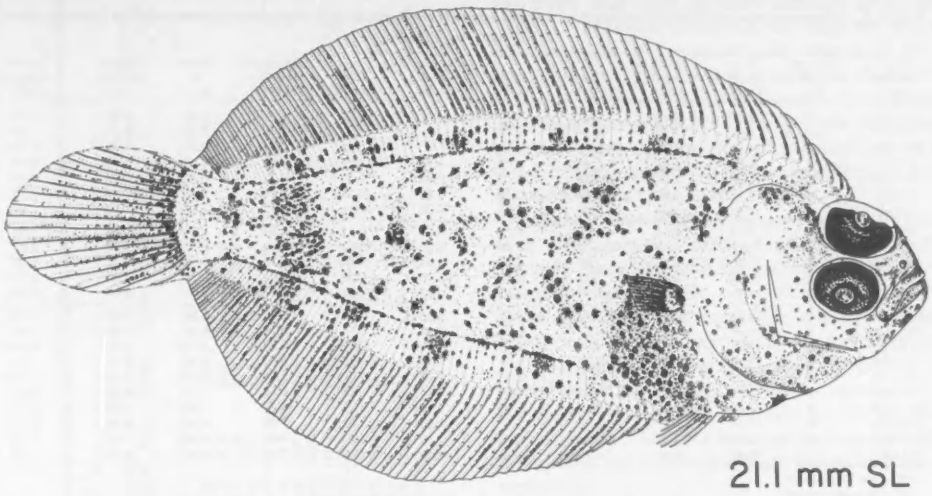

FIGURE 5.—Recently transformed benthic juvenile *Isopsetta isolepis*, 21.1 mm SL.

be due to the different environmental conditions of the reared and planktonic larvae. With development the gut continues to coil and the hindgut, which is initially directed posteriorly, comes to rest in an anteriorly directed position, by about 17 mm.

Notochord flexion begins by the time larvae are about 9 or 10 mm long and the notochord is fully flexed by about 14 mm. After flexion is complete, the tip of the urostyle continues to extend beyond the hypural plate, sometimes until larvae are 17 mm long. When larvae are about 12 or 13 mm long, near the end of notochord flexion, the left eye begins to migrate to the right side of the head. The left eye is visible on the ridge of the head, when viewed from the right side, in some larvae as small as 15 mm and consistently in specimens >17 mm. The left eye eventually migrates to the degree that it is directed upward, the most advanced position before complete transformation to benthic juvenile. This was the most advanced stage of eye migration of specimens taken in plankton tows and was observed in some, but not all, specimens >20 mm. The largest specimen collected in the plankton was 23.6 mm, but the most developed plankton specimen in terms of eye migration and increased pigmentation was 21.9 mm. The smallest specimen collected in a beam trawl was 18.0 mm, but its eye was on the dorsal ridge of the head directed upward and it had not completed transformation. The smallest benthic juvenile, in which the left eye had crossed over the middorsal ridge and juvenile pigment had intensified on the eyed side, was 18.5 mm.

With development (Tables 2, 3), relative head length increases considerably from mean values of 13-15% SL in preflexion larvae to 25% SL in postflexion larvae. Snout to anus length remains essentially constant with respect to standard length with mean values of 29-32%. Relative body depths at the pectoral fin base, at the anus, and behind the anus increase dramatically through the larval period with mean values nearly doubling in most cases between preflexion and flexion stages and doubling again between flexion and postflexion stages. The greatest rate of increase occurs in the depth behind the anus. Depth of the caudal peduncle also increases from 3 to 10% relative to standard length. Relative eye diameter is largest in preflexion larvae (29-36% HL (head length)) and decreases in flexion (24% HL) and postflexion (22% HL) larvae as does the relative length of the upper jaw (37-25% HL).

Ossification of Meristic Structures

Descriptions, based on cleared and stained specimens, depict only general trends of development because the size at which bones begin to ossify may vary among specimens and the uptake

TABLE 2.—Measurements (millimeters) of plankton caught larvae of *Isopsetta isolepis*. (Specimens between dashed lines are undergoing notochord flexion.)

Length interval (mm)	Sample size (*N*)	Mean length (mm)	Snout to anus	Head length	Snout length	Upper jaw length	Eye diameter	Body depth at pectoral fin base	Depth at anus	Depth behind anus	Caudal peduncle depth
2.9-3.0	2	2.90	0.95	0.45	—	—	0.20	0.30	0.20	0.15	0.10
3.1-4.0	[1]6	3.67	1.07	0.50	0.10	—	0.20	0.40	0.30	0.17	0.10
4.1-5.0	[2]4	4.63	1.28	0.55	0.10	—	0.25	0.40	0.35	0.23	0.10
5.1-6.0	[3]5	5.50	1.48	0.68	0.10	0.30	0.28	0.50	0.46	0.22	0.10
6.1-7.0	[4]5	6.58	2.04	1.02	0.12	0.40	0.30	0.72	0.72	0.34	0.12
7.1-8.0	[5]5	7.76	2.20	1.14	0.10	0.43	0.32	1.04	1.00	0.44	0.16
8.1-9.0	6	8.77	2.58	1.32	0.10	0.48	0.38	1.17	1.12	0.50	0.28
9.1-10.0	4	9.68	2.88	1.48	0.20	0.50	0.45	1.25	1.23	0.60	0.35
10.1-11.0	6	10.57	3.42	1.95	0.28	0.62	0.48	1.72	1.68	1.25	0.60
11.1-12.0	4	11.25	3.38	1.88	0.20	0.60	0.50	1.78	1.72	1.15	0.55
12.1-13.0	5	12.36	3.70	2.24	0.28	0.76	0.50	2.02	2.14	1.54	0.74
13.1-14.0	5	13.55	4.22	2.74	0.36	0.72	0.62	2.52	3.12	2.08	0.96
14.1-15.0	5	14.48	4.84	3.18	0.50	0.86	0.64	3.18	3.68	3.00	1.34
15.1-16.0	5	15.38	4.68	3.58	0.54	0.94	0.74	3.74	4.40	3.64	1.48
16.1-17.0	5	16.54	5.64	4.00	0.60	1.10	0.90	4.64	5.36	4.84	1.68
17.1-18.0	5	17.50	5.88	4.70	0.78	1.12	1.10	5.60	6.16	6.00	1.86
18.1-19.0	4	18.63	5.85	4.78	0.93	1.28	1.08	6.43	6.85	6.95	1.88
19.1-20.0	6	19.55	5.92	4.93	0.94	1.20	1.08	6.52	7.00	6.90	2.02
20.1-21.0	6	20.53	5.97	5.12	0.95	1.28	1.10	6.90	7.35	7.50	2.03
21.1-22.0	4	21.48	6.40	5.93	0.95	1.60	1.23	7.68	8.18	8.58	2.23
22.1-23.0	6	22.48	6.27	5.58	0.95	1.22	1.23	7.67	8.33	8.62	2.28
23.1-24.0	4	23.33	6.80	5.68	0.98	1.43	1.25	7.83	8.48	9.03	2.33

[1]N = 2 for snout length.
[2]N = 3 for snout length.
[3]N = 4 for snout length and 1 for upper jaw length.
[4]N = 1 for upper jaw length.
[5]N = 4 for upper jaw length.

TABLE 3.—Body proportions of *Isopsetta isolepis* larvae. Values given are percentages: mean ± standard deviation, and range in parentheses.

Item	Preflexion larvae with yolk (reared)	Preflexion larvae without yolk (reared)	Preflexion larvae without yolk (plankton)	Flexion larvae (plankton)	Postflexion larvae (plankton)
No. measured	20	42	[1]37	[2]20	50
SL	(2.7-4.0)	(3.4-5.4)	(2.9-9.0)	(10.5-14.2)	(13.5-23.6)
Head length/SL	15.0±2.7(10.6-19.6)	13.4±0.9(11.3-15.9)	14.2±2.0(10.2-17.2)	18.3±1.6(15.3-20.7)	24.9±2.1(20.7-29.4)
Snout to anus length/SL	32.4±3.8(28.3-39.3)	28.8±1.3(26.7-31.1)	29.2±2.9(22.9-34.4)	30.7±1.8(27.6-34.0)	31.0±3.0(23.2-35.8)
Depth at pectoral fins/SL	5.2±0.8(4.1-6.7)	9.2±1.0(7.4-11.6)	11.4±2.3(8.3-15.2)	16.6±1.7(12.9-18.5)	31.1±5.0(20.1-38.0)
Depth at anus/SL	9.8±1.2(8.2-12.0)	8.9±0.9(6.9-11.1)	10.3±2.8(5.7-15.6)	17.8±3.7(12.9-28.9)	34.1±4.4(23.2-40.2)
Depth behind anus/SL	4.3±0.7(2.8-5.9)	3.2±0.5(2.5-4.1)	5.1±1.3(2.9-7.8)	12.3±2.0(9.0-14.8)	33.4±6.7(18.8-41.3)
Caudal peduncle depth/SL	—	—	2.6±0.8(1.3-4.1)	6.0±1.1(4.4-7.4)	9.6±2.0(7.6-11.3)
Eye diameter/HL	32.8±2.6(30.2-38.1)	28.9±3.9(21.6-39.6)	35.6±9.1(25.0-50.0)	23.7±2.8(20.0-29.4)	21.8±2.2(17.5-26.2)
Snout length/HL	19.9±6.0(9.4-29.8)	28.1±4.1(20.8-34.0)	12.5±4.4(6.7-20.0)	13.7±2.8(8.7-21.0)	16.6±3.7(9.4-20.8)
Upper jaw length/HL	—	—	37.1±4.9(31.2-50.0)	31.6±5.9(24.0-47.6)	25.2±4.4(17.5-38.5)

[1]Except N = 29 for snout length and N = 16 for upper jaw length.
[2]Except N = 19 for snout length.

of stain may be affected by length of preservation. Terminology of bones generally follows Richardson and Joseph (1973) and Frame et al. (1978) except as noted.

Most of the meristic characters of *I. isolepis* larvae begin ossifying during notochord flexion (10-14 mm); only gill rakers and pectoral fin rays begin to ossify at larger sizes (Table 4; Figure 6). The following discussion roughly parallels the sequence of development of meristic characters, and we note their first appearance as well as the onset of ossification as indicated by the acceptance of Alizarin Red stain.

Paired conical teeth may be observed on the dentary of 5.3 mm larvae, and on the premaxillaries by 5.8 mm. Teeth continue to increase in number as the larvae grow. Teeth are consistently more numerous on the left (ultimately the blind) side of the head than the right side. The smallest specimen in which teeth accepted alizarin stain was 12 mm, possibly an artifact of preservation. Larval teeth develop in approximately two nonparallel rows. The outer row consists of conical, caninelike teeth, and the inner row is composed of smaller, curved teeth. Most teeth are ossified in 18 mm larvae. By transformation (ca. 20.0 mm), butter sole larvae possess approximately 37 larval teeth on the left dentary (27 in the outer row; 10 smaller teeth on an inner row) and about 37 large conical teeth on the left premaxillary arranged in

TABLE 4.—Development of meristic structures in *Isopsetta isolepis* larvae. Mean data are given for larvae in the specified length range. (Specimens between dashed lines are undergoing notochord flexion.)

SL (mm)	Sample size	Dorsal fin rays	Anal fin rays	Caudal fin rays	Pectoral fin rays		Pelvic fin rays		Neural spines			Haemal spines	Centra			Branchiostegal rays	Gill rakers	
					Left	Right	Left	Right	Abdom.	Caudal	Total		Abdom.	Caudal	Total		Upper	Lower
3.2-8.9	50	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.0-9.9	5	—	—	1.8	—	—	—	—	—	—	—	—	—	—	—	0.8	—	—
10.0-10.9	12	—	—	4.4	—	—	—	—	2.0	9.2	11.2	9.2	—	—	—	1.8	—	—
11.0-11.9	12	11.6	9.2	10.7	—	—	0.3	0.3	5.7	20.8	26.5	20.8	0.8	2.8	3.6	5.0	—	—
12.0-12.9	15	19.6	17.2	14.9	—	—	—	—	8.9	26.7	35.6	26.5	0.3	4.2	4.3	6.0	—	—
13.0-13.9	17	51.8	34.8	15.5	—	—	0.9	0.9	8.1	27.5	35.6	27.5	3.5	16.3	19.8	5.9	—	—
14.0-14.9	18	45.0	36.8	14.6	—	—	0.4	0.4	9.1	27.1	36.2	27.0	4.9	19.0	23.9	6.1	—	—
15.0-15.9	17	52.9	46.8	15.4	—	—	2.2	2.2	8.2	24.8	33.0	24.8	6.4	22.0	28.6	5.6	—	—
16.0-16.9	10	72.2	55.0	18.0	—	—	2.1	2.1	9.9	30.5	40.4	30.5	9.9	31.8	41.7	7.0	—	—
17.0-17.9	11	89.7	67.5	18.0	0.5	0.5	4.5	4.5	10.0	31.2	41.2	31.2	10.0	32.2	42.2	7.0	—	—
18.0-18.9	15	87.3	66.9	18.0	0.7	0.7	5.0	5.0	9.9	30.9	40.8	30.9	9.9	31.9	41.7	7.0	—	0.3
19.0-19.9	9	87.9	67.9	18.0	0.3	0.3	6.0	6.0	9.9	31.2	41.1	31.0	9.9	32.0	41.9	7.0	—	—
20.0-20.9	9	88.0	68.1	18.0	1.8	1.8	6.0	6.0	9.9	30.9	40.8	30.8	9.9	31.7	41.6	7.0	—	1.7
21.0-21.9	4	88.8	67.8	18.0	2.3	2.3	6.0	6.0	10.0	30.8	40.8	30.8	10.0	31.8	41.8	7.0	—	1.0
22.0-22.9	5	91.2	68.8	18.0	5.0	5.0	6.0	6.0	10.0	31.0	41.0	30.8	10.0	31.8	41.8	7.0	—	2.8

two rows. The right dentary contains about 20 teeth (11 large conical teeth in the outer row and 9 smaller teeth in the inner row). The right premaxillary contains nine larger teeth and six smaller teeth. Teeth continue to increase in number after transformation. A 44 mm juvenile possessed about 40 teeth each on the left premaxillary and left dentary and 14 teeth on the right dentary and 10 teeth on the right premaxillary.

Neural spines ossify during notochord flexion (Table 4; Figure 6). The first neural spine to ossify lies just above the first haemal spine in the anterior abdominal region, and ossification proceeds posteriorly and anteriorly. The last two neural spines to ossify are those on the antepenultimate and penultimate vertebrae. Ossification is usually completed at about 16.5 mm. Haemal spines ossify from anterior to posterior beginning with the first haemal spine. The last two haemal spines to ossify are also on the antepenultimate and penultimate vertebrae.

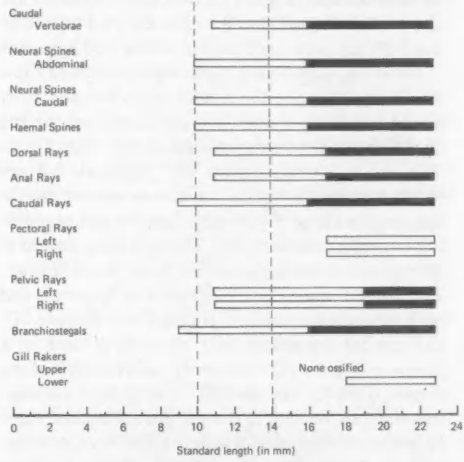

FIGURE 6.—Diagrammatic summary of the sequence of ossification of principal meristic structures in *Isopsetta isolepis*. Dashed vertical lines indicate size range in which notochord flexion occurs; open bars indicate meristic structure is undergoing ossification; solid bars indicate meristic structure is completely ossified.

In the axial skeleton the first centrum to ossify (as early as 11 mm) supports the first haemal spine. Ossification proceeds both anteriorly and posteriorly, with the urostyle ossifying before the antepenultimate and penultimate vertebrae. All centra are ossified by 17 mm.

The first caudal supports to ossify are hypurals[10] 2 and 3 in larvae as small as 12 mm. Hypural 1 is ossified by 13 mm and hypural 4 at about 15 mm. The epurals ossify last at about 16 mm. We interpret the caudal complex of *I. isolepis* to consist of four hypurals (two below and two above the medial axis) and two epurals. One is a normal-sized epural that supports the uppermost caudal ray, and the other epurallike bone is reduced in size and supports no rays (Figure 6H). No uroneurals are present.

Fin rays begin to ossify during notochord flexion (10-14 mm) in the dorsal, anal, caudal, and pelvic fins. Ossification is completed in the following order: caudal, dorsal, anal, pelvic, and pectoral fins (Table 4; Figure 6). Pectoral fin rays were not fully ossified in the largest stained larva, 22.8 mm.

The anlage of the base of the caudal fin begins to form by 5.5 mm (Figure 7A). Incipient caudal rays are evident from 5.5 to 8.8 mm. By 10.5 mm (Figure 7 B) the notochord begins to flex and hypurals 1-3 develop, supporting about eight incipient rays. At about 12.7 mm the notochord is usually fully flexed and three hypurals are evident, supporting 10 differentiated but unossified caudal rays (Figure 7C). By 14.3 mm (Figure 7D), hypurals 1-3 are ossified and some caudal rays have started ossifying, beginning at the center of the fin and proceeding dorsally and ventrally. The full complement of 18 rays is consistently ossified by 16.4 mm (Figure 7E). By 18.0 mm (Figure 7F) all four hypurals and both epurals are ossified. By 22.8 mm (Figure 7G) the caudal fin essentially resembles that of a juvenile (Figure 7H) and nearly all elements of the caudal complex are ossified. The 18 rays, consisting of (from ventral to dorsal) 3 unbranched rays, 12 branched rays, and 3 unbranched rays, are carried on the hypurals as follows: epural 1, 1 ray; hypural 4, 2 rays; hypural 3, 6 rays; hypural 2, 5 rays; hypural 1, 4 rays.

Incipient dorsal fin rays may be observed in the proximal portion of the finfold at midbody by 10.5 mm. Ossification of dorsal rays begins at midbody by 11 mm and proceeds anteriorly and posteriorly. By 17.5 mm the dorsal rays reach their full complement and are completely ossified.

The anal fin develops in a manner analagous to the dorsal fin and nearly simultaneously. Rays begin to differentiate at midbody with formation progressing both anteriorly and posteriorly. Ossified rays begin at midbody at about 11 mm and the full complement may be ossified by 17.5 mm.

Pelvic fin buds may be observed on larvae as small as 10 mm, although not consistently until notochord flexion is complete at about 14 mm, and individual rays may begin ossifying by 11 mm. The full complement of six rays is ossified by 19 mm.

Pectoral fin buds are visible above the yolk sac in newly hatched reared larvae. Larval pectoral fins are present in the smallest stained larvae examined (3.2 mm). The rays begin to differentiate by 13.5 mm and individual rays begin ossifying as transformation occurs by about 17 mm. The full complement of pectoral rays was not attained in the largest larva examined, 22.8 mm, but is fully developed in a 44 mm juvenile.

Branchiostegal rays begin to accept alizarin stain at about 9.5 mm. The adult complement of seven rays may be differentiated, but not ossified, by 13.6 mm. All rays are ossified by 16 mm.

Gill rakers on the first ceratobranchial begin forming at about 7 mm. A maximum of six rakers was formed in the largest stained larva examined (22.8 mm). No rakers were formed on the epibranchials of this specimen. The adult complement of four plus seven gill rakers is present on a 44 mm juvenile.

Of the median fin supports, pterygiophores supporting anal and dorsal fin rays begin ossifying at about 19 mm. These pterygiophores are completely ossified by 22.8 mm (Figure 8).

Scales form sometime between 22.8 mm (largest stained larva) and 44 mm (smallest stained juvenile).

OCCURRENCE

Off Oregon, larvae of *I. isolepis* are distributed mainly in the near coastal zone within 18 km of shore, with abundance peaks at 6-9 km (Richardson 1973, see footnote 4; Richardson and Pearcy 1977). Smaller numbers of larvae have been taken as far as 56 km offshore (Richardson and Pearcy 1977; Laroche and Richardson 1979), inside the mouth of Yaquina Bay (Pearcy and

[10]We follow Moser and Ahlstrom's (1970) definition of hypurals ". . . all bones of hypaxial origin associated with ural centra [are defined] as hypurals, including the lowermost bone."

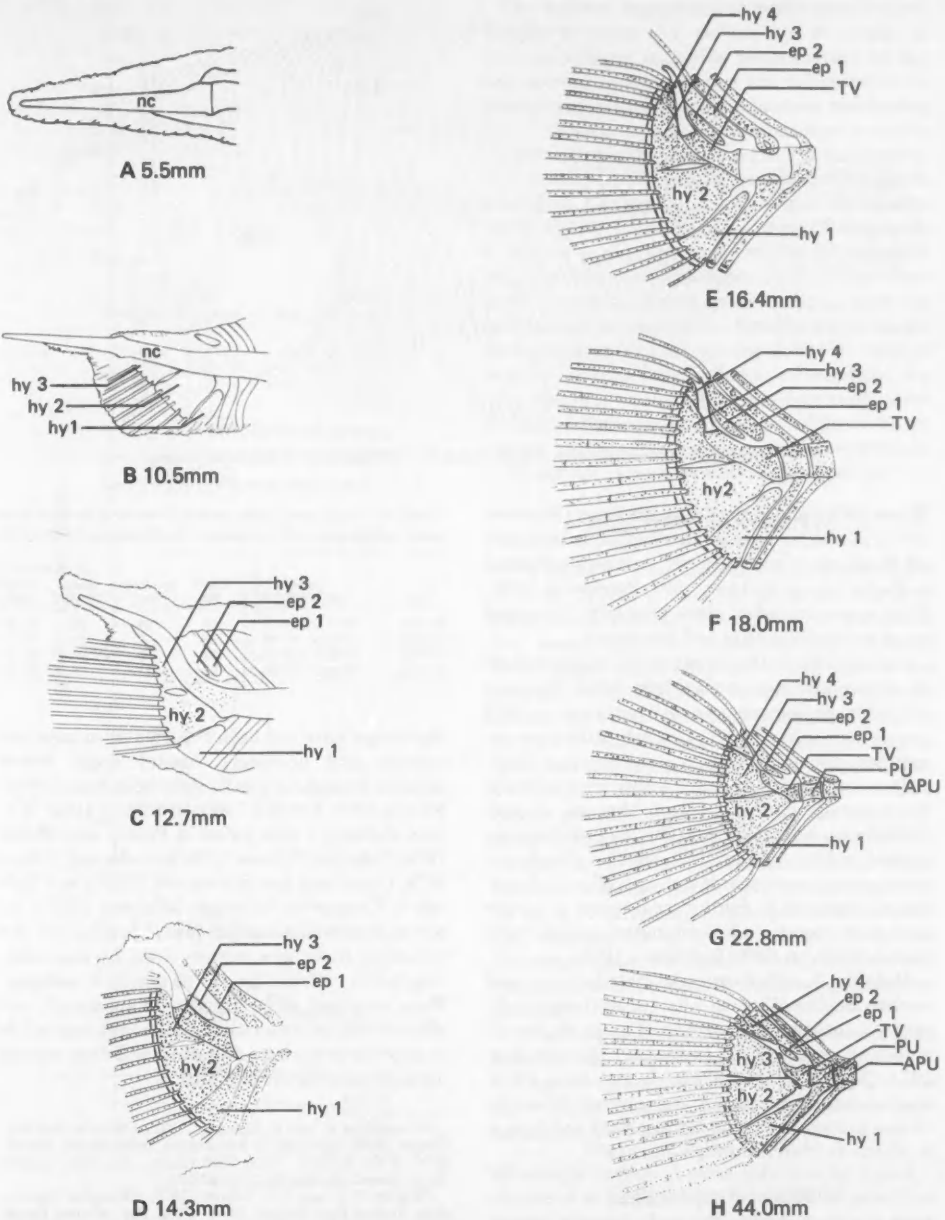

FIGURE 7.—Development of the caudal fin of *Isopsetta isolepis*: 5.5 mm SL, 10.5 mm SL, 12.7 mm SL, 14.3 mm SL, 16.4 mm SL, 18.0 mm SL, 22.8 mm SL, and 44.0 mm SL. Ossified elements are stippled. hy = hypurals; ep = epurals; nc = notochord; APU = antepenultimate vertebrae; PU = penultimate vertebrae; TV = terminal vertebrae.

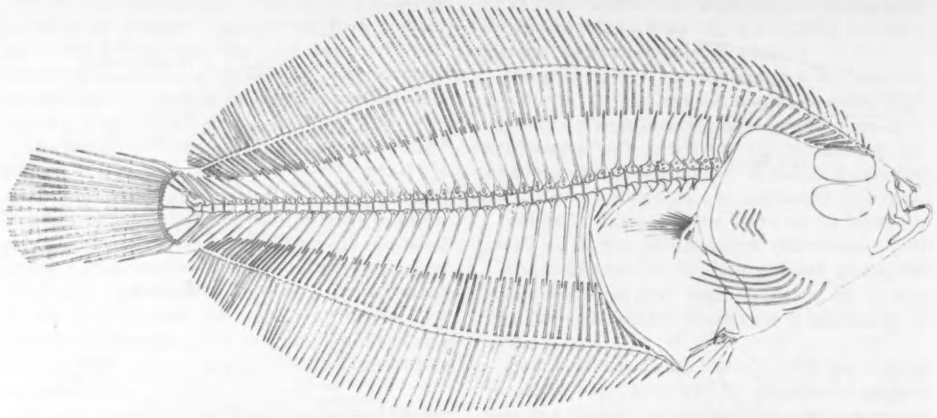

FIGURE 8.—Juvenile *Isopsetta isolepis*, 44 mm SL, showing details of skeletal structure.

Myers 1974), and in the Columbia River (Misitano 1977). A similar coastal distribution is indicated off Washington with reduced numbers occurring in Puget Sound (Waldron 1972; Blackburn 1973). Thus spawning takes place primarily in coastal areas rather than bays and estuaries.

Larvae occur in the plankton off Oregon mainly in winter and spring (Waldron 1972; Misitano 1977; Richardson see footnote 4) although in 1971 larvae were taken in every month of the year except September, November, and December (Richardson see footnote 4). In 1972 they were taken in every month sampled, March through August (Richardson see footnote 4). In 1971, abundance peaked in May, and in 1972, smaller abundance peaks were observed in March and May (Richardson see footnote 4). Spring occurrences of larvae have been reported off Washington and in Puget Sound (Waldron 1972; Blackburn 1973).

Monthly length-frequency distributions and median lengths of larvae collected off Oregon indicate winter-spring spawning (Figure 9). Small larvae <5 mm were taken January through May 1971, October 1971, and March and April 1972. Median lengths increased progressively from 2 to 16 mm in January through June 1971 and from 4 to 16 mm in March through June 1972.

Based on available data, *I. isolepis* apparently settles to the bottom in coastal areas and remains near the coast during the early juvenile period. Newly transformed juveniles (18-38 mm) have been collected off the mouth of the Columbia River in depths of 34-56 m (Table 5). Juveniles in this size range have not been reported from bays, estuaries, and nearshore coastal areas where juvenile *Parophrys vetulus* have been found (Westrheim 1955; Kendall 1966; Beardsley 1969; William Johnson's data listed in Pearcy and Myers 1974; Peden and Wilson 1976; Laroche and Holton 1979; Cummings and Schwartz[11]; Higley and Holton[12]; Krygier[13]). Although Misitano (1977) reported that both *I. isolepis* and *P. vetulus* use the Columbia River as a nursery area, he was referring to fish >85 mm long (>95 mm for *I. isolepis*). Thus, smaller *I. isolepis* juveniles apparently use offshore coastal areas during their first year of life as opposed to the bay, estuarine, and near coastal nursery habitats of *P. vetulus*.

TABLE 5.—Data from beam trawl collections of juvenile *Isopsetta isolepis* taken off the mouth of the Columbia River, 1975.

Date	Location (Lat. N, long. W)	Depth (m)	Specimens (no.)	SL of larvae	
				Median (mm)	Range (mm)
26 June	46°11.5', 124°07.6'	37	86	24	18-38
26 June	46°09.5', 124°06.3'	40	7	21	18-24
14 Sept.	46°09.5', 124°05.0'	34	5	24	22-26
15 Sept.	46°09.3', 124°08.0'	56	11	25	20-28

[11]Cummings, E., and E. Schwartz. 1971. Fish in Coos Bay, Oregon, with comments on distribution, temperature, and salinity of the estuary. Oreg. Fish Comm., Res. Div., Coastal Rivers Invest. Inf. Rep. 70-11, 22 p.

[12]Higley, D. L., and R. L. Holton. 1975. Biological baseline data, Youngs Bay, Oregon, 1974. Final Rep. Alumex Pacific Aluminum Corp., 1 November 1973 through 30 April 1975. Oreg. State Univ., Sch. Oceanogr. Ref. 75-6, 91 p.

[13]E. Krygier, Research Assistant, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. June 1978.

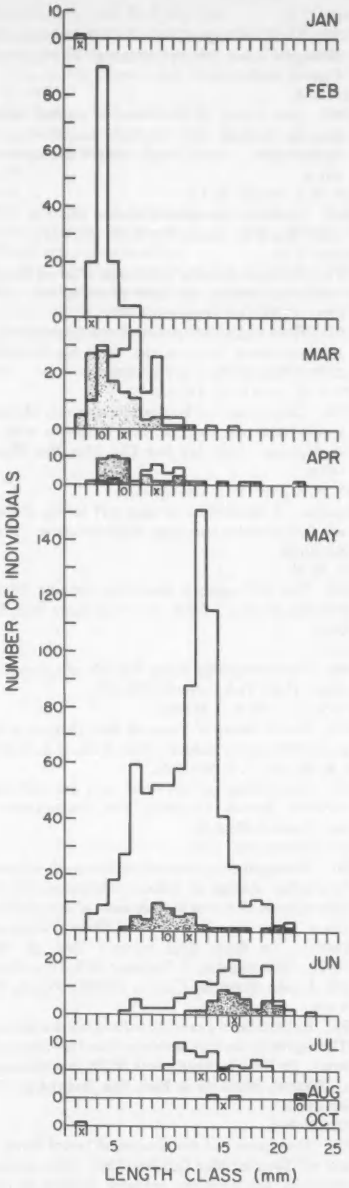

FIGURE 9.—Length-frequency histograms of *Isopsetta isolepis* larvae collected in 70 cm bongo nets off Oregon in 1971 (unshaded) and 1972 (shaded). X = median length of larvae in 1971; 0 = median length of larvae in 1972.

The habitat separation of newly transformed benthic juveniles of *I. isolepis* and *P. vetulus* is interesting since spawning times overlap for the two species and the larvae are codominants in coastal waters off Oregon (Richardson and Pearcy 1977). Habitat separation also has been noted in large (>10 mm) larvae; *P. vetulus* is more abundant in neuston samples relative to plankton samples than *I. isopsetta* (Laroche and Richardson 1979). Ratios of relative abundance of *P. vetulus* to *I. isolepis* in plankton samples was 2:1 compared with 36:1 in neuston samples. Thus the two cooccurring species appear to be utilizing different parts of the water column. Smaller larvae might be segregated similarly by depth, but we have no data on vertical distribution to substantiate this idea. Feeding studies, which may help verify these habitat differences and provide evidence for resource partitioning between these morphologically similar larvae, remain to be conducted.

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RETENTION OF THREE TAXA OF POSTLARVAL FISHES IN AN INTENSIVELY FLUSHED TIDAL ESTUARY, CAPE FEAR RIVER, NORTH CAROLINA

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ABSTRACT

Fixed nets were used to sample postlarvae of spot, *Leiostomus xanthurus*, Atlantic croaker, *Micropogonias undulatus*, and flounders, *Paralichthys* spp., over several 24-hour periods in the Cape Fear River, near Wilmington, North Carolina. Results of analyses of variance on abundance data collected at two locations indicate that these taxa exhibit distinct behavioral responses, primarily to photoperiod and tide, which allow them to maintain a selected position in the estuary and avoid being flushed seaward. The level of response to these variables dictates ultimate residence in at least two primary nurseries, the river main stem in the vicinity of the salt boundary and the tidal salt marshes. By migrating to the surface at night, both spot and flounders make apparent use of tides to augment lateral migration into marshes. Conversely, by tending to remain more bottom oriented at all times, Atlantic croaker accumulate in greater numbers in deep water at the head of the estuary.

Mechanisms by which larval fishes are recruited to, and concentrated in, estuaries are poorly understood. Attempts to elucidate these mechanisms suffered from the generally high degree of variability associated with sampling larval fish populations. Recognizing this, Graham (1972) employed fixed nets to collect larval Atlantic herring, *Clupea harengus*, in the Sheepscot estuary of Maine. His gear offered the advantage of obtaining synoptic samples over the entire water column, and because much greater volumes were filtered, the variability of the data was also reduced. Consequently, he was able to infer a mechanism used by Atlantic herring larvae to select a specific reach of the estuary, i.e., a behavioral response manifested by interactions between depth, or location, and tidal direction.

The importance of such interactions has not always been fully appreciated; e.g., Pearcy and Richards (1962) postulated that larval fish transport in the Mystic estuary occurred mainly in the lower layer by net nontidal flows. Similarly, Haven (1957) and Sandifer (1975) described utilization of net nontidal transport in the lower layers for fishes and invertebrates in the Chesapeake Bay. However, these investigators collected larvae during the daytime only and did not consider diel migrations which may bring many larvae to the surface at night (Pacheco and Grant 1968; Lewis and Wilkens 1971; Williams and Porter 1971). Moreover, certain larval fishes (e.g., menhaden) may also frequent the upper layers to a considerable extent during the day (Thayer et al. in press). Thus, it is probable that the retention mechanism is species-specific and involves several elements as described by Bousfield (1955): 1) diel changes in vertical distribution; 2) utilization of the residual, or nontidal, drift seaward in the upper layer and landward along the bottom; and 3) changing behavioral parameters with respect to tidal direction (e.g., see also Hughes 1969a, b, 1972; Turgeon 1976). Individual species may utilize one or more of these mechanisms to reach and stay within a preferred zone of the estuary, from its mouth (Carriker 1951) to the headwaters (Haven 1957; Turgeon 1976).

Here we describe distributions of postlarval fishes in two locations within the Cape Fear River estuary, near Southport, N.C. Both sampling areas were situated upriver, in an area believed to constitute a primary nursery zone for several fish species. Sampling was stratified by location, depth, photoperiod, and tidal direction, and an attempt was made to depict postlarval fish behavior with respect to these strata. A hypothesis is

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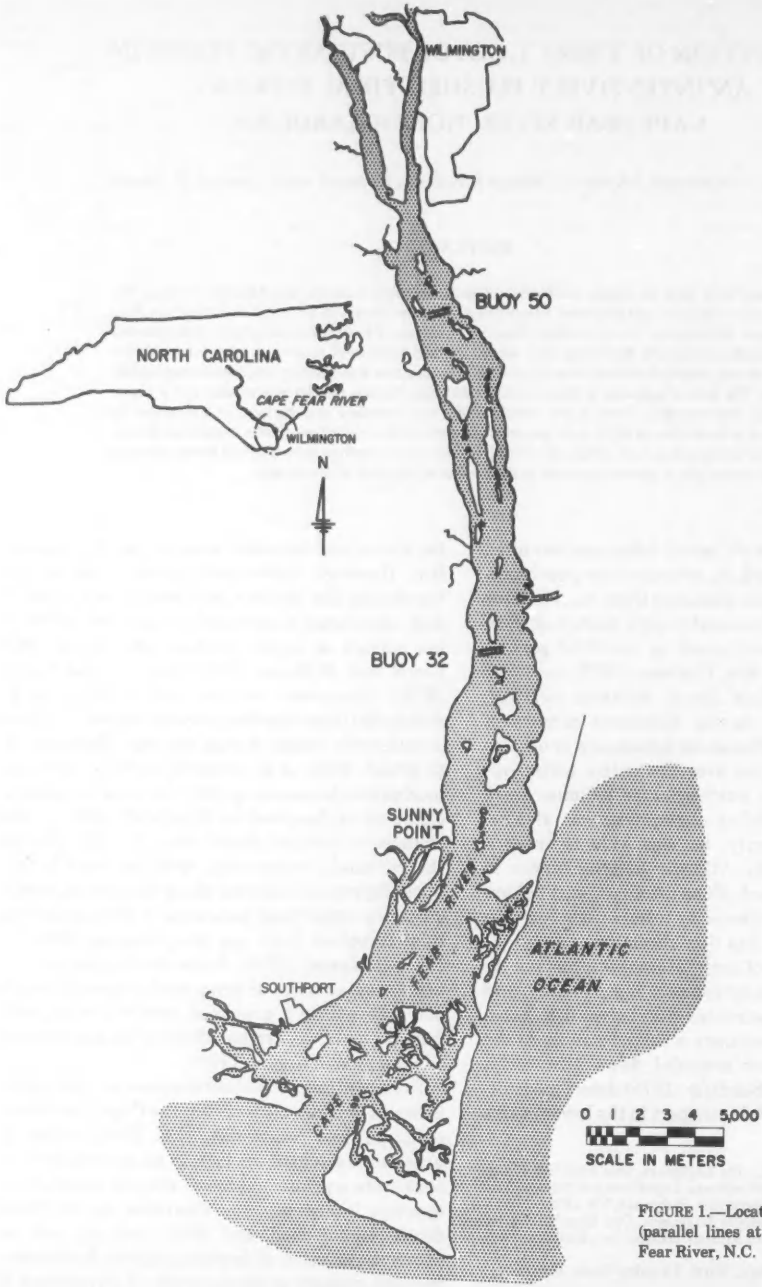

FIGURE 1.—Location of sampling transects (parallel lines at bouys 32 and 50), Cape Fear River, N.C.

formulated which relates these behavioral responses to the maintenance of a preferred position within the estuary.

STUDY AREA

The Cape Fear River estuary (approximately lat. 33° N) is relatively narrow, averaging only 1.6-3.6 km in width and extending 45 km from the general location of the salt boundary at Wilmington, N.C., to the river mouth at Baldhead-Smith Island (Figure 1). A 12 m deep ship channel with a width of 120-150 m is maintained from Wilmington to the river entrance, and adjacent spoil islands are found along its entire length. Tidal velocities in the Cape Fear are high, averaging 2.1 m/s during ebb near the city of Southport, N.C. (National Ocean Survey 1977). Recent hydrographic and dye studies (Carpenter[4]) have established that a two-layer system occurs in the estuary between the vicinity of Sunny Point and Wilmington (Figure 1).

Extensive tidal salt marshes cover about 8,900 ha and form the largest contiguous system of this type in the State of North Carolina (U.S. Army Corps of Engineers[5]). Tidal creeks cover an estimated 648 ha, and shallow open water areas (shoals) between the channel and salt marshes contribute an additional 7,285 ha of suitable nursery habitats for the young of fishes and shellfish.

MATERIALS AND METHODS

A modified version of the gear designed by Graham (1972) was employed in this study (Figure 2A). Individual 0.5 m plankton nets with stainless steel cod end buckets were suspended from aluminum collars (Figure 2B) and bolted onto orienting vanes attached to a 9.5 mm diam-

[4]Carpenter, J. H. 1979. Dye tracer and current meter studies, Cape Fear Estuary 1976, 1977 and 1978. Final report to the Carolina Power & Light Co., Raleigh, N.C., 339 p.

[5]U.S. Army Corps of Engineers. 1977. Maintenance of Wilmington Harbor, North Carolina. Final environmental statement. U.S. Army Engineers District, Wilmington, N.C., 97 p.

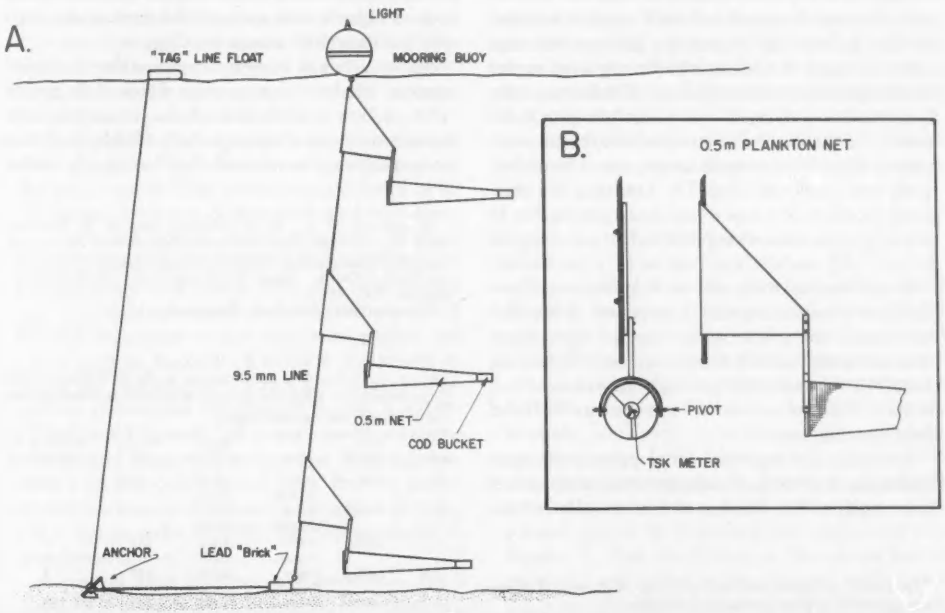

FIGURE 2.—A. Sampling apparatus and deployment, the middepth nets were not used on the east and west shoals. B. Detail of the orienting vane and net mounting. Paired meters were used on all bottom nets.

eter nylon rope. Tidal flows in the Cape Fear estuary were sufficiently high to fully extend these nets during the sampling period. Lead weights (66 kg) between the anchor and bottom net were used to fix the depth at which the bottom nets fished, and a tag line and float attached to the anchor shaft allowed each rig to be easily retrieved at the end of the sampling period. Surface nets were rigged to sample at 1.5 m below the surface, mid-depth nets at a depth of 6.5 m (in the main channel), and bottom nets, approximately 1 m above the substrate. In order to reduce detection by postlarvae, all nets were dyed deep brown (Rit[6] #20, Cocoa Brown—W. Watson[7]).

Samples were collected at two locations on three sets of dates: 14-15 March, 5-6 April, and 11-12 April. A pair of closely spaced transects were situated near river buoy 50, close to the head of the estuary, and another pair at river buoy 32, at Snow's Cut (Figure 1). Two vessels were employed on each sampling date, and for each transect, three stations were established across the main channel from east to west. At slack water the east and west shoal rigs were set first in 7.6 m of water, and the channel station nets were anchored last. All nets at each of the paired transects were set in <40 min. Because the period of slack water continued for the duration of the setting process, the nets actually began to fish simultaneously and, except for the period of retrieval (about 20 min), a nearly synoptic set of samples was taken across a cross section of the main channel and shoals. On each pair of dates four consecutive tides were sampled, with nets retrieved after 2 h. Limiting the sampling period to 2 h was a necessary precaution in this study because of the potential for net clogging in the highly turbid Cape Fear estuary (see below).

It was planned to sample two nighttime and two daytime tides during each survey but, due to differences in the predicted and actual tides, there was sufficient ambient light to read field data sheets by the end of the last night set at buoy 50 on 6 April. For this reason, the sample was excluded from the analyses.

To reduce the potential for clogging, nets were constructed of 752 μm mesh material and tapered to a length of 3 m. Meshes of this size allowed the passage of many small plankton as well as fine detritus, but retained the postlarvae [≈7-34 mm SL (standard length)] of interest. Previous studies of comparative length frequency in 505 and 760 μm nets (Copeland et al.[8]) indicated that postlarvae <7 mm (of the species of interest) were uncommon in the Cape Fear estuary, since they were recruited from well offshore.

In a preliminary experiment in November 1976, five nets were fished near the bottom, off a tidal creek bridge, and pulled sequentially every 0.5 h after an initial fishing period of approximately 1.0 h (Table 1). The flow past each net was monitored by a TSK[9] meter mounted in the center of the mouth of each net and by a second meter affixed to the collar support. After more than 3 continuous hours of fishing at relatively low flows (compared with the main channel), clogging, as determined by the difference between the inside and outside meter readings, did not exceed 28% on the last net pulled. However, a piece of filamentous algae was found wrapped around the inner TSK prop and axle on this net, restricting free movement. Meter fouling caused by fibrous detritus and algae along the river bottom created considerable difficulties in obtaining useful bottom meter readings in the actual experiments and was deemed a more serious problem than severe net clogging.

In an attempt to overcome bias due to fouled meters, all bottom nets were fitted with paired TSK meters as described above. Based upon the results of the preliminary study (Table 1), it was conservatively estimated that an inside meter

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[7]W. Watson, Associate, Cape Fear Estuarine Laboratory, North Carolina State University, Southport, N.C., pers. commun. September 1976.

[8]Copeland, B. J., R. G. Hodson, and R. J. Monroe. 1979. Larvae and postlarvae in the Cape Fear River estuary, North Carolina, during operation of the Brunswick Steam Electric Plant, 1974-78. Report 79-3 to Carolina Power & Light Co., Raleigh, N.C., 214 p.

[9]Tsurumi Seiki Kosakusho Company.

TABLE 1.—Preliminary net clogging study at Walden Creek, Cape Fear River. Negative percentage difference indicates that inside meter reading was largest.

Net	Time retrieved	Meter	Meter revolutions	Volume (m^3)	% difference (inside/outside)
1	1235	Inside	3,053	97	5
		Outside	3,214		
2	1305	Inside	8,633	275	3
		Outside	8,896		
3	1336	Inside	6,822	217	−7
		Outside	6,357		
4	1406	Inside	14,402	458	9
		Outside	15,812		
5	1437	Inside	12,565	[1]400	28
		Outside	17,410		

[1]A piece of filamentous algae was found wrapped around the TSK prop and axle, restricting free movement.

reading <80% of the outside reading would indicate that the inside meter had fouled. Of the 144 bottom samples collected, 71 had low inside meter readings and 16 had high inside readings. An additional 3 samples were discarded due to gear failure, leaving a total of 54 samples that could be used to obtain an estimator for volume.

A strong linear relationship between inside and outside meter readings ($r = 0.996$, $P<0.01$) indicated that an adequate linear predictor could be obtained:

$$Y = 0.913\,X$$

where Y is the inside meter reading and X is the outside meter reading, both in revolutions. The standard error of the slope of this line is 0.009, and the standard error of an individual estimate of the inner reading is:

$$\mathrm{SE} = \sqrt{7.4729 \times 10^{-5}\,X^2 + 1.758337 \times 10^{6}}\ .$$

The above estimator was used to obtain volumes for all bottom samples in which the inside meter reading was <80% of the outside reading. If a net were actually clogged when we assumed that the meter was fouled, this procedure would result in an overestimate of the volume filtered and underestimate of the actual density of larvae present. Thus, differences among strata would be even larger than depicted in our data.

Upstream and downstream nets at each depth along the paired transects served as replicates in the experiments. This survey constituted a factorial design, with site, photoperiod, and tidal direction as main effects. Nonorthogonal factorial analyses of variance (ANOVA) (Searle 1971) were performed for each taxon, date, and buoy (except spot and Atlantic croaker at buoy 50 on 14-15 March). Examples of the analytical results are reproduced in Appendix I to allow the reader to follow our procedures. A posteriori multiple comparison procedures (Bonferroni t-tests $\alpha = 0.05$; O'Neill and Wetherill 1971) were used to examine station and depth differences and their interactions with photoperiods and tides. Prior to analysis, data were logarithmically transformed [$\log_{10}(10 + X)$] in order to meet the homoscedasticity requirement of ANOVA.

A partial data analysis was performed for 5 April 1978 at buoy 50, deleting the last night set. Either daytime or ebb data alone were used, depending on the strata compared. However, data from all three valid sets were used to obtain an estimate of sampling variability.

All collections were preserved in 5% buffered Formalin, and selected taxa were enumerated and measured for standard length (SL). The latter measurement was taken from the tip of the snout to the end of the notochord or hypural plate. Subsampling for lengths was employed when sorted collections contained >100 individuals of a given species. Data are presented herein on three taxa: spot, *Leiostomus xanthurus*; Atlantic croaker, *Micropogonias undulatus*; and flounders of the genus *Paralichthys*. Flounders were counted but not measured in this program.

RESULTS

Since the April sampling dates were near the end of recruitment for winter-spawned species in the Cape Fear estuary, the observed pattern of distribution during this month should reflect the selection of preferred nursery habitats. On 14-15 March, freshwater flow in the river exceeded 990 m^3/s, and the salt boundary was below buoy 50, as indicated by the absence of measurable salt in the water column. On these dates, spot were entirely absent at buoy 50 and only two Atlantic croaker postlarvae were captured (Figures 3, 4). Flounders, however, were abundant at buoy 50 during this period. When subsequent sampling indicated that the salt front was restored to its normal location, about 6 km above buoy 50, catches of all taxa (with one exception) were significantly greater ($P<0.05$) upstream (Table 2).

Diel Behavior

Significant differences were only occasionally detected among stations and were likely influenced by local patterns of current and larval transport. For this reason, these comparisons were not considered further and were omitted from the ANOVA summary (Table 3). Consistant trends, however, were evident in several other comparisons involving depth, photoperiod, and their interactions. For example, the 24 h mean abundance across depths for spot and Atlantic croaker, and to a lesser degree for flounders, was higher (see also Figures 3, 4) at the bottom on the shoals and at middepth and below in the channel, with essentially no differences between buoys. Photoperiod, on the other hand, influenced the catches of flounder in a consistent manner. Except for 14-15

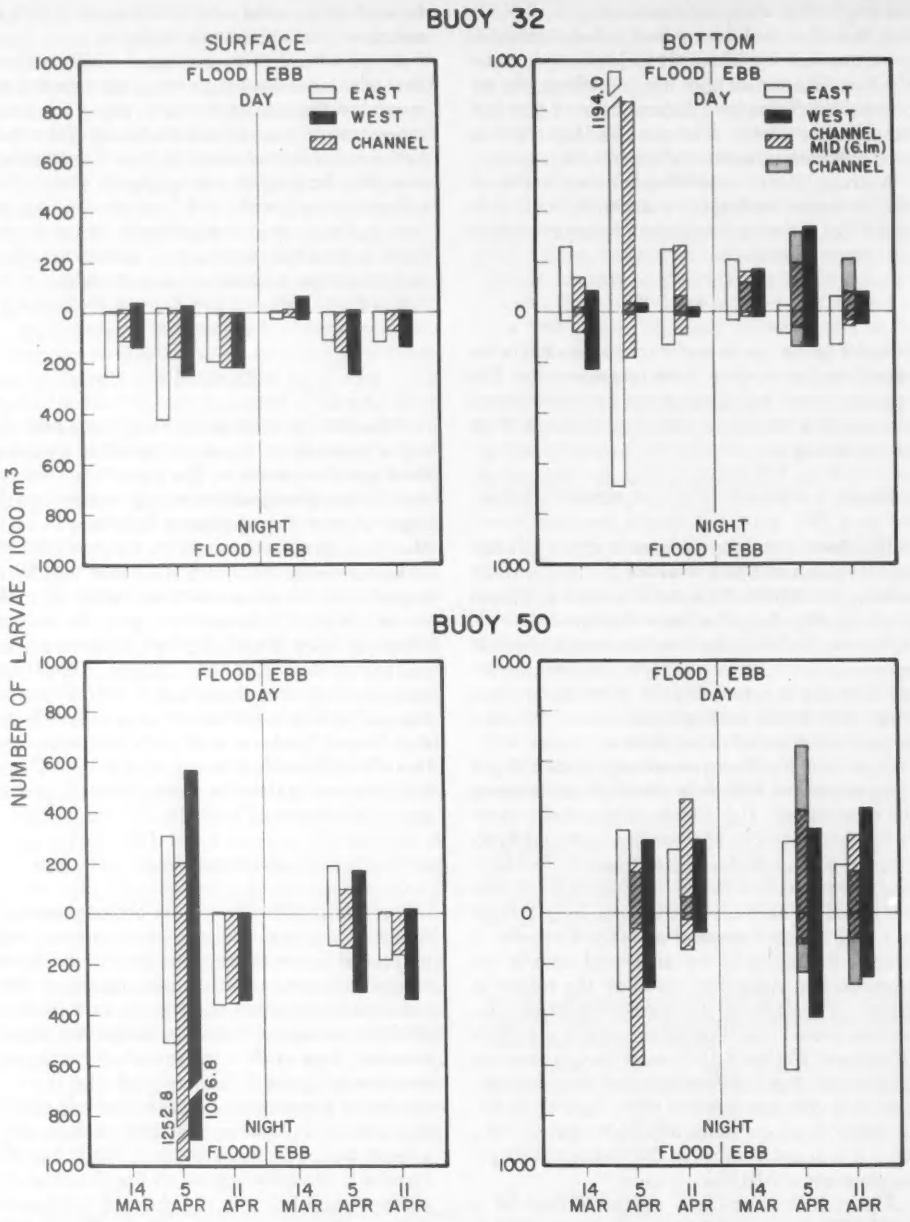

FIGURE 3.—Abundance of spot, *Leiostomus xanthurus*, collected on three sampling dates at buoys 32 and 50. Data are stratified to show mean values for each paired transect with respect to surface-bottom, day-night, and flood-ebb catches. Spot were not captured at buoy 50 on 14-15 March.

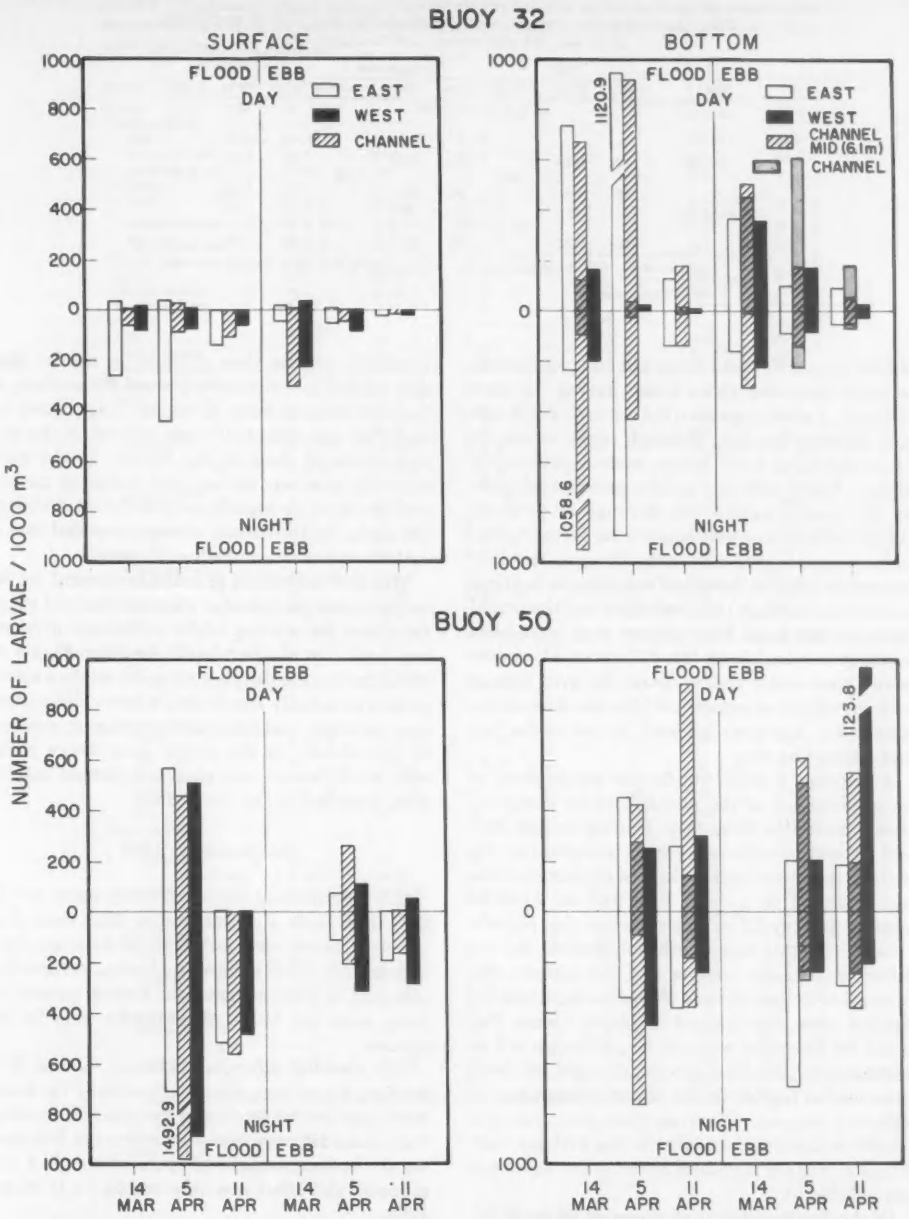

FIGURE 4.—Abundance of Atlantic croaker, *Micropogonias undulatus*, collected on three sampling dates at buoys 32 and 50. Data are stratified to show mean values for each paired transect with respect to surface-bottom, day-night, and flood-ebb catches. Only two croaker were captured at buoy 50 on 14-15 March, these are not shown.

TABLE 2.—Comparison of mean density (number/1,000 m³) at buoy 32 versus buoy 50 for spot, Atlantic croaker, and *Paralichthys* spp.

Date	Spot			Atlantic croaker			*Paralichthys* spp.		
	Buoy	Mean	*t*-value	Buoy	Mean	*t*-value	Buoy	Mean	*t*-value
14-15 Mar.	No analysis conducted						32	46.7	14.76*
							50	147.8	
5-6 Apr.[1]	32	193.4	7.85*	32	189.4	11.55*	32	17.3	1.40
	50	302.7		50	329.3		50	18.0	
11-12 Apr.	32	89.1	8.91*	32	52.6	4.79*	32	2.3	3.64*
	50	179.2		50	294.9		50	3.9	

*Significant at $\alpha = 0.05$; transformed log(10 + X) data utilizing error mean squares from initial ANOVA's.
[1]Last night set omitted.

March at buoy 50 and 5-6 April at buoy 32, catches at night exceeded those taken during daylight (Table 3). A similar pattern did not emerge for spot and Atlantic croaker, although night values on 11-12 April at both buoys were significantly higher. Apparently, net avoidance was negligible in this study, unlike the findings of Graham (1972), who limited his sampling for larval Atlantic herring to night hours in the Sheepscot estuary because of what he described as excessive daytime net avoidance. High tidal velocities and the turbid waters of the Cape Fear estuary may have been partially responsible for this difference. Flounders were either better able to detect the dyed nets or perhaps exhibited somewhat different diurnal behavior; e.g., a greater tendency to rest on the bottom during the day.

A response to light was further established by an examination of the photoperiod by depth interactions for the three taxa. During the day, spot and Atlantic croaker were most abundant at the bottom and at middepth. Only in the partial data sets analyzed on 5 April 1978 and for Atlantic croaker at buoy 32 on this date was this pattern changed. On this date, depth distributions did not differ for Atlantic croaker and the surface concentration for spot at buoy 50 was not significantly smaller than the channel middepth value. The trend for flounders was similar, although not as distinct as for the other species. At night, all three taxa moved higher in the water column but to differing degrees. Whereas flounders and spot tended to congregate nearer to the surface, most Atlantic croaker remained lower in the water column (Table 3).

Of the five significant photoperiod by depth interactions involving flounders, a posteriori tests conducted for night data indicated that surface concentrations in four instances were significantly greater than at all other depths. Spot also tended to accumulate toward the surface, on the two dates at buoy 32 where a significant interaction was detected, night catches at the surface exceeded those at the bottom; in the main channel, however, surface and middepth concentrations were not significantly different, although the mean for the former always exceeded that of bottom values by a substantial margin.

The best indication of a diel movement by Atlantic croaker occurred in the main channel where the mean for surface night collections diverged less from that of other depths (see also Figure 4), while during the day, the mean for surface collections was usually significantly lower. No surface accumulation was detected for Atlantic croakers on the shoals, on the single date where a significant difference was observed, bottom catches were greater than at the surface.

Response to Tide

Ebb tide catches were generally lower for all taxa than those of corresponding flood tides (Figures 3-5). In addition, a shift in catch density from channel middepth toward the bottom occurred on ebb, and in several instances bottom concentrations exceeded those of middepth nets for all species.

The observed difference between ebb and flood concentrations was always significant for flounders, and on two occasions, for Atlantic croaker. Tide alone did not seem to exert a major influence on the concentrations of spot, although a significant tidal effect was observed on 14-15 March 1978.

All three taxa displayed a trend towards larger flood catches on the eastern shoal and in the channel, while on ebb the western shoal often exhibited

TABLE 3.—Analyses of variance summary, for stations (depths), photoperiod and tides. Station as a main effect is omitted and not all possible interactions are shown. Multiple comparison test results are shown below individual letter designations.

Source		Buoy 32			Buoy 50		
		14 March	5 April	11 April	14 March	5 April[1]	11 April
Depths[2]							
East/west							
Spot		B>S	B>S	B>S	—	(B>S)	B>S
Atlantic croaker		B>S	B>S	B>S	—	(B>S)	B>S
Paralichthys spp.		B>S	ns[3]	ns	ns	(ns)	ns
Channel							
Spot		M B S	M B S	M B S	—	(B M S)	M B S
Atlantic croaker		M B S	M B S	M B S	—	(ns)	M B S
Paralichthys spp.		M S B	ns	ns	ns	(ns)	ns
Photoperiod[4]							
Spot		ns	D>N	N>D	—	(ns)	N>D
Atlantic croaker		ns	D>N	N>D	—	(ns)	N>D
Paralichthys spp.		N>D	D>N	N>D	ns	(N>D)	N>D
Tides[5]							
Spot		F>E	ns	ns	—	(ns)	ns
Atlantic croaker		ns	ns	F>E	—	(F>E)	ns
Paralichthys spp.		F>E	F>E	F>E	F>E	(F>E)	F>E
Photoperiod × depth							
Spot							
East/west	D	B>S	B>S	B>S	—	(ns)	B>S
	N	ns	S>B	S>B	—	(ns)	ns
Channel	D	M B S	M B S	M B S	—	(B M S)	M B S
	N	S M B	S M B	S M B	—	(ns)	S M B
Atlantic croaker							
East/west	D	B>S	B>S	B>S	—	(ns)	B>S
	N	B>S	ns	ns	—	(ns)	ns
Channel	D	M B S	M B S	M B S	—	(ns)	M B S
	N	M B S	ns	M S B	—	(ns)	ns
Paralichthys spp.							
East/west	D	B>S	B>S	ns	ns	(ns)	B>S
	N	ns	S>B	S>B	ns	(ns)	ns
Channel	D	M B S	M B S	M B S	ns	(ns)	ns
	N	M S B	S M B	ns	ns	(ns)	S M B
Tide × station[6]							
Spot							
Flood		E W C	E C W	E C W	—	[ns]	ns
Ebb		ns	W C E	ns	—	[ns]	W C E
Atlantic croaker							
Flood		E C W	E C W	E C W	—	[ns]	ns
Ebb		ns	C W E	C E W	—	[C W E]	W C E
Paralichthys spp.							
Flood		E C W	E C W	ns	ns	[ns]	ns
Ebb		ns	ns	ns	ns	[ns]	W E C
Tide × depth							
Spot							
East/west	F	ns	ns	ns	—	[ns]	ns
	Ebb	B>S	B>S	B>S	—	[ns]	B>S
Channel	F	M S B	M S B	M S B	—	[ns]	M S B
	Ebb	ns	B M S	B M S	—	[B M S]	B M S
Atlantic croaker							
East/west	F	B>S	ns	ns	—	[ns]	B>S
	Ebb	B>S	B>S	B>S	—	[ns]	B>S
Channel	F	M B S	M S B	M S B	—	[ns]	M S B
	Ebb	M B S	B M S	B M S	—	[ns]	M B S
Paralichthys spp.							
East/west	F	ns	ns	ns	ns	[ns]	ns
	Ebb	ns	ns	ns	ns	[ns]	ns
Channel	F	M S B	M S B	ns	ns	[ns]	ns
	Ebb	ns	ns	ns	ns	[ns]	ns

[1][ ]—daytime data only from partial data set on 5 April; ( )—ebb tide data only from partial data set.
[2]Depths: surface (S), middepth (M), bottom (B).
[3]ns—no significant difference at $\alpha = 0.05$ level.
[4]Photoperiods: day (D), night (N).
[5]Tides: flood (F), ebb (E).
[6]Stations: east (E), channel (C), west (W).

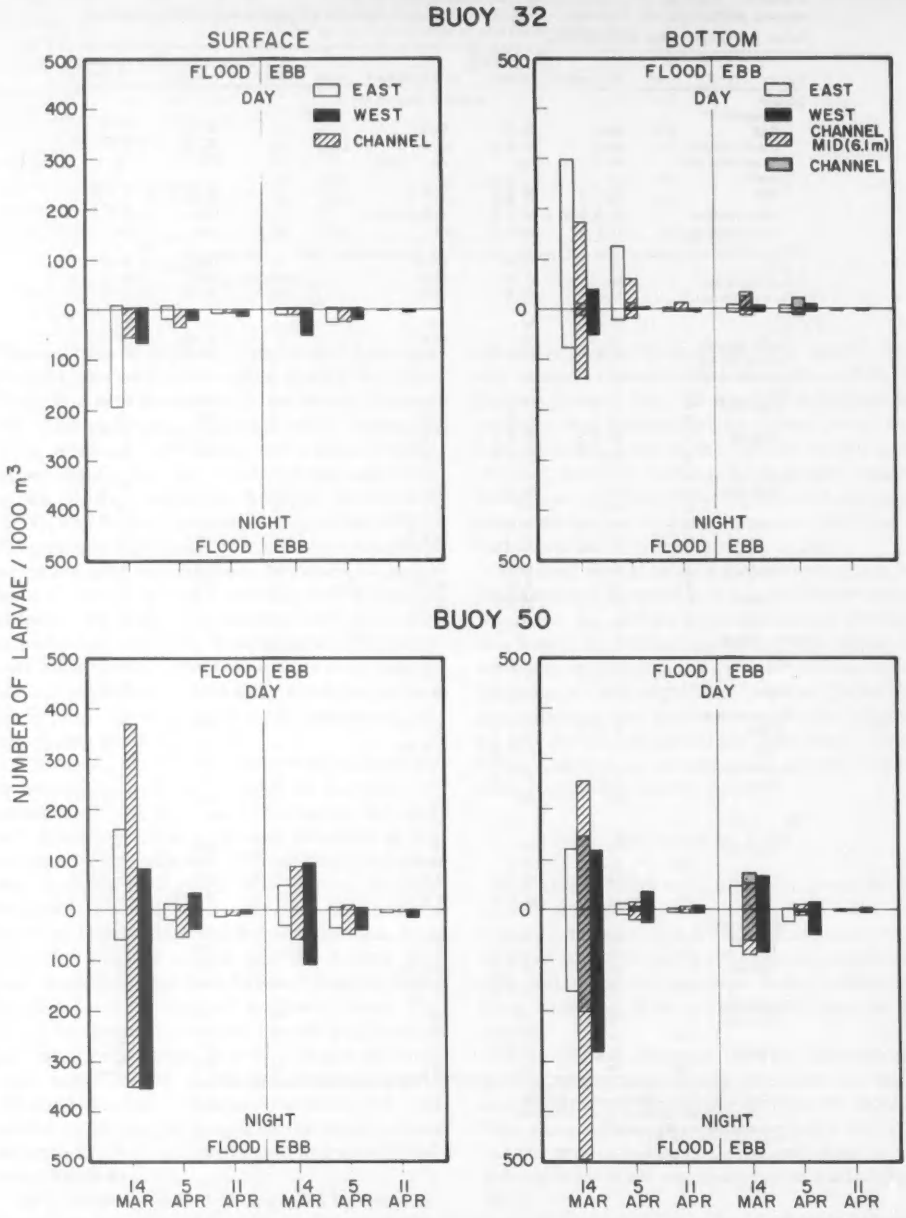

FIGURE 5.—Abundance of flounders (*Paralichthys* spp.) collected on three sampling dates at buoys 32 and 50. Data are stratified to shown mean values for each paired transect with respect to surface-bottom, day-night, and flood-ebb catches.

the largest mean catch. This pattern paralleled the flow of river water between tides; i.e., water tended to move upriver on the eastern shoal and returned on the west. If this phenomenon is real, it indicates the existence of a large-scale circulation pattern for postlarval populations.

The tide by depth interaction clearly described the immediate relationship of these organisms to tidal flows. Whereas the depth distribution of spot on flood tides was fairly uniform, bottom and mid-depth concentrations on ebb often exceeded those of surface values. Results were not quite as clear for Atlantic croaker because of their general bottom orientation; nevertheless, a tidal response was still evident for this species (Figure 4). Paradoxically, flounder showed little response to tide (compared with the main effect result), although a pattern similar to that of the other species is shown in the mean concentrations in Figure 5.

All of these comparisons are potentially influenced by diel activity, i.e., by downward migration during the day. Mean bottom values are influenced by this effect on both flood and ebb during daylight hours. One way of isolating the effect of photoperiod would be to examine the interaction of the three main effects (Table 3). Unfortunately, this interaction was rarely significant. Lack of significance may be a consequence of the use of a logarithmic scale in making comparisons. Also, the power of tests on this three-way interaction is considerably less than that of tests of main effects and of two-way interactions. That diel migration was not entirely responsible for the observed patterns may be seen in the overall (24 h) differences between flood and ebb. Since two flood and ebb tides were sampled over each 24-h period, the effect of diel activity should be manifested on both tides; i.e., bottom orientation should occur on flood as well. Table 3 indicates that this was not the case. Furthermore, a perusal of the individual strata in Figures 3-5; e.g., an examination of surface night concentrations alone, shows that a clear tidal response was exhibited by all three species.

Length-Frequency Distributions

The possibility that buoy 50 was located within a primary nursery zone was alluded to earlier. This contention is also supported by length-frequency data which show that larger (older) fish tended to accumulate upriver near buoy 50. Unfortunately, larger fishes were probably not captured quantitatively since gear efficiency drops off rapidly after about 30 mm SL (Copeland et al. see footnote 8). Hence, only a qualitative picture of the age composition of a year class is possible. Nevertheless, distinct size differences occurred between buoys as indicated in Figures 6 and 7.

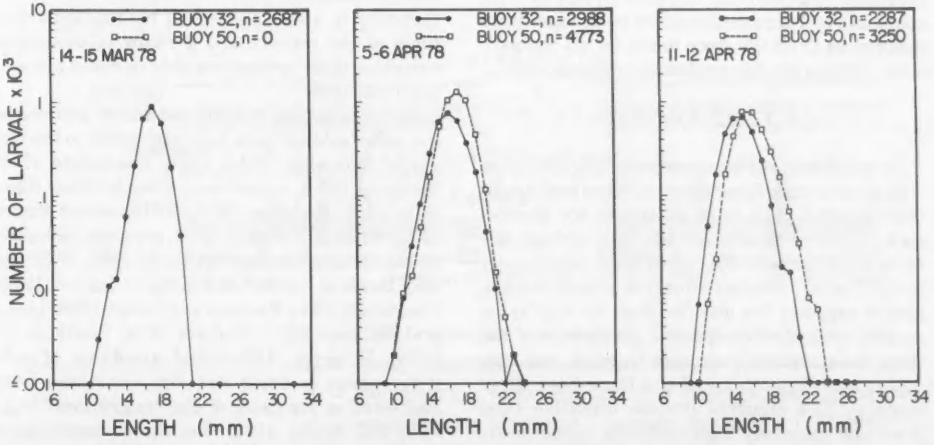

FIGURE 6.—Length-frequency distribution for spot, *Leiostomus xanthurus*, on the three collecting dates. This species was entirely absent from the vicinity of buoy 50 on 14-15 March.

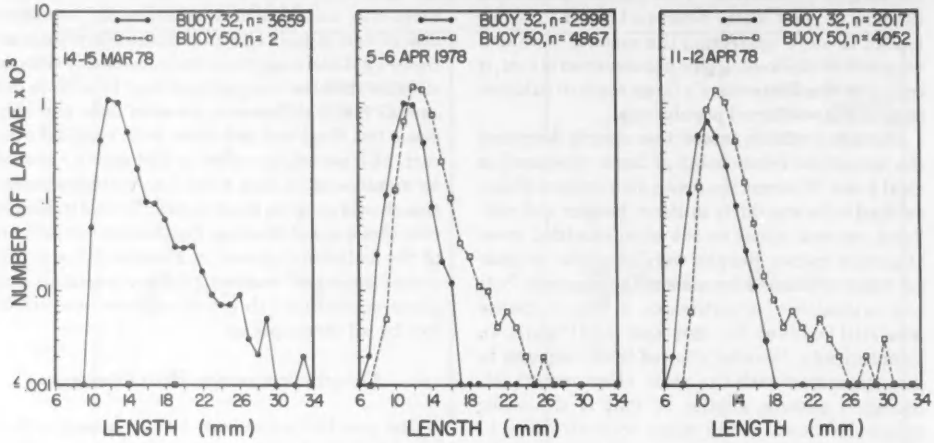

FIGURE 7.—Length-frequency distribution for Atlantic croaker, *Micropogonias undulatus*, on the three collecting dates. Only two individuals were captured in the vicinity of buoy 50 on 14-15 March.

Most interestingly, during the high-flow period on 14-15 March 1978, when spot and Atlantic croaker moved downriver, the larger fish accompanied the newer recruits to the vicinity of buoy 32. This is most evident in Figure 7 for Atlantic croaker. With the return of the salt front above buoy 50 in April, spot and Atlantic croaker returned upstream. For both species in this month, length-frequency distributions at buoys 32 and 50 were compared by Pearson chi-square tests. Significant differences ($P<0.05$) were found for all comparisons, with larger fish predominating upstream.

DISCUSSION

In contemplating the retention of bivalve larvae within the James River estuary, Wood and Hargis (1971) stated, "The point at issue is not whether such retention occurs, but whether evolved patterns of larval behaviour contribute significantly to the process." Evidence from the present investigation supports the premise that, by displaying specific behavioral responses, postlarvae of the three taxa studied were able to reach and stay within specific portions of the Cape Fear River estuary. This occurred despite intensive tidal flows and relatively high exchange ratios in the system.

Peak recruitment for winter-spawned larvae in the Cape Fear estuary and many other Atlantic coast estuaries occurs at a time when stratification and tidal exchange ratios are usually at a yearly maximum. The exchange ratio may exceed 0.70 in the Cape Fear estuary and flows above 1,700 m^3/s have been recorded in January and February 1978 (Carpenter see footnote 4). Species recruited from the ocean also have the peculiar problem of initial entrance into the estuary and the avoidance of being washed out on the subsequent tide. By responding to a combination of hydrographic features of the estuary and perhaps to exogenous variables these species are able to avoid net seaward transport.

Active responses to light and diel migrations in the water column have been attributed to the larvae of barnacles (Fales 1928; Bassindale 1936; Bousfield 1955), oysters and other bivalves (Carriker 1951; Korringa 1952; Williams and Porter 1971: Wood and Hargis 1971), copepods (Schallek 1943), shrimp (Hughes 1969a, b, 1972; Williams and Deubler 1968), and fishes (Rogers 1940; Creutzberg 1961; Pacheco and Grant 1968; Lewis and Wilkens 1971; Graham 1972; Smith et al. 1978). However, differential avoidance of nets with respect to depth has also sometimes been suggested as the cause of diel "migrations" (e.g., Fore and Baxter 1972). Results of comparative studies using several kinds of collecting gear, including high-speed trawls (Thayer et al. in press), and the observed absence or low abundance of

most species (including those studied here) in daylight entrainment collections at a power plant located on the river near Southport (Copeland et al. see footnote 8) imply that this hypothesis is not tenable and support the contention that diel migrations actually do take place. If larvae were similarly stratified in the water column with respect to tide, a result paralleling that of the photoperiod response would be expected. By resting on the substratum during ebb, or at least by moving downward in the water column (below the level of no net motion), larvae would be transported in the landward direction.

Behavioral responses of spot, Atlantic croaker, and flounders to photoperiod and tide are summarized in Figure 8. Several important differences delineate ultimate habitat utilization by these species. Flounders apparently reacted to tidal flows by settling to the bottom, as has been suggested for oysters and shrimps (Carriker 1951; Hughes 1969a, b, 1972). When the lack of significant tide by depth interaction and the presence of a tidal main effect are considered together, this hypothesis seems more tenable. To a degree, seeking boundary layers may be a general tidal response exhibited by all three species, making them difficult to sample on ebb (especially since the bottom nets were set 1 m above the substrate). The ability of flounders to effectively penetrate freshwaters also is enhanced by this behavior. Tidal flows above the salt boundary are substantial, certainly greater than the ability of flounder postlarvae to negotiate them directly. Saltatory movement upriver by "riding out" ebb on the bottom and responding to currents on flood would then be a primary mechanism for continued upstream migration.

Both spot and flounders were also observed to migrate toward the surface at night; significantly larger numbers of individuals were captured in this stratum both in midchannel and on the shoals, while Atlantic croaker tended to remain

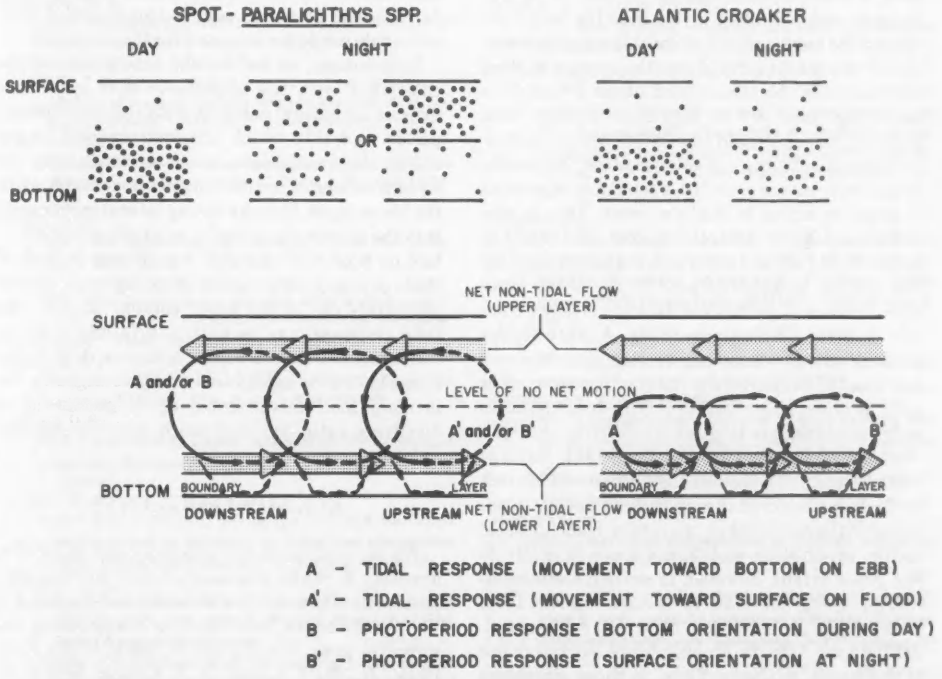

FIGURE 8.—Conceptual model for a larval retention mechanism based on response to photoperiod and tide. Details of the response differ for the three taxa (see text).

bottom oriented during this period. In studies of feeding by postlarval fishes in the Newport River estuary, N.C., Peters and Kjelson (1975) and Kjelson et al. (1975) demonstrated that spot were actively feeding only during the daytime and described them as carnivorous sight feeders. If the nighttime surface orientation observed for flounders and spot is not related to feeding activity, then to what might it be attributed?

We suggest that active migration into the marshes is aided by surface movement on flood tide at night. Since the mouths of many of these tidal creeks have sills, and since most are shallow and lack stratification, remaining near the bottom in the main stem would not aid postlarvae in lateral movements into the marshes. However, by staying near the surface on night flood tides, large numbers of individuals would be carried laterally into the marshes and other shoal areas, perhaps with the additional advantage of lower predation pressure.

Once in the marsh or other suitable shallow area, a tidal response elicited on ebb, i.e., a tendency to seek boundary layers near the bottom or toward the banks, would allow at least some members of the cohort carried into the system on flood to remain on ebb (Lewis and Mann 1971). This percentage need not be very high on each tidal cycle to produce a rapid population accumulation.

Species displaying a greater tendency to remain in the lower layers over 24 h should not be present in great numbers in shallow areas. This is precisely the case for Atlantic croaker. The marshes in the Cape Fear are not a major nursery zone for this species, as demonstrated by the nearly complete absence of postlarval Atlantic croaker from this habitat (Weinstein 1979). A noteworthy paradox arises when this species is considered over most of its geographic range. Atlantic croaker seem to prefer those estuaries with deep channels and are not taken in large numbers in the shallows (Welsh and Breder 1923; Wallace 1941; Suttkus 1955; Haven 1957; Nelson 1969; Chao and Musick 1977). It is suspected that in these estuaries, postlarval Atlantic croaker maintain their general bottom orientation and do not move laterally to any great extent; however, in several shallow estuaries along the Gulf of Mexico (Herke 1971; Parker 1971; Arnoldi et al. 1974; Yakupzack et al. 1977) young Atlantic croaker make extensive use of the marsh shallows. Thus, in those situations where deep channels are not predominant features of the system, Atlantic croaker will make use of the marsh shallows. This difference in distribution in the Gulf States might be further reconciled if temperature is taken into consideration. Temperature as a potential limiting factor for Atlantic croaker year class success in most middle Atlantic coast estuaries has been discussed by Joseph (1972). Remaining in the warmer waters of the deep channel during winter might enhance Atlantic croaker survival. The winters of 1976-77 and 1977-78 along the Atlantic coast have been colder than usual; greater utilization of shallow areas by Atlantic croaker might occur in warmer years.

Others also have observed that the river main stem at the head of the Cape Fear estuary is a primary nursery zone for Atlantic croaker and, to a more limited extent, for spot and flounders (Copeland et al. see footnote 8). In addition, the boundaries of this zone for certain species are dictated by freshwater flows and tend to shift with these flows. Although not captured quantitatively, larger spot and Atlantic croaker accumulated upriver in the vicinity of buoy 50 (Figures 6, 7). Although flounders were not measured, a similar result would be expected for these species.

In summary, we believe the data presented are consistent with the hypothesis that postlarvae exhibit behavioral patterns with respect to photoperiod and tide which are instrumental in enabling these organisms to: 1) accumulate in upstream nurseries by utilizing net nontidal flows in the lower layer, 2) make strong lateral movements into the marsh nurseries by migrating to the surface on flood tide at night, and 3) stay in both of these primary nurseries by dropping lower into or effectively out of the water column on ebb. The tidal response may be particularly important in well-mixed estuaries where upstream drift in the lower layers is negligible. In fact, it might be the primary mechanism employed by postlarvae to penetrate estuaries and reach suitable nursery habitats.

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APPENDIX TABLE 1.—Three-way analysis of variance for spot, *Leiostomus xanthurus*, postlarvae captured at buoy 32, 14-15 March 1978. Catch data are $\log_{10}(10 + X)$ transformed.

Source	df	SS	MS	*F*	Source	df	SS	MS	*F*
Photoperiod, P	1	0.0551	0.0551	1.50	P × S	6	3.2729	0.5455	14.83*
Tide, T	1	0.2218	0.2218	6.03*	T × S	6	0.5744	0.9057	2.60*
Sites, S	6	2.6871	0.4479	12.17*	P × T × S	6	0.3805	0.0634	1.72
P × T	1	1.2493	1.2493	33.95*	Error	24	0.8831	0.0368	

Multiple comparisons (Numbers in parentheses are mean catch for each stratum.)

A. Tides
Flood (100.7) > ebb (68.2)

B. Sites (Bonferroni *t*-tests; $\alpha = 0.05$)
1. Depths: east and west
Bottom (131.9) > surface (68.3)
2. Depths: channel
Largest: middepth(97.1) bottom (39.3) surface(39.2): smallest
3. Stations
Largest: east(109.5) west(90.6) channel(58.5): smallest

C. Photoperiod × tide (Bonferroni *t*-tests; $\alpha = 0.05$)
Largest: flood/night(120.3) ebb/day(103.3) flood/day(81.1) ebb/night (27.2): smallest

D. Photoperiod × site (bonferroni *t*-tests; $\alpha = 0.05$)
1. Photoperiod × depth: east and west
Day: bottom(178.5) > surface(25.0)
Night: ns[1]
2. Photoperiod × depth: channel
Day; largest: middepth(145.0) bottom(65.9) surface(8.8): smallest
Night; largest: surface(79.5) middepth(49.2) bottom(3.9): smallest
3. Photoperiod × station
Day: ns
Night; largest: west(97.8) east(91.1) channel(44.3): smallest

E. Tide × site (Bonferroni *t*-tests; $\alpha = 0.05$)
1. Tide × depth: east and west
Flood: ns
Ebb: bottom(112.6) > surface(31.3)
2. Tide × depth: channel
Flood; largest: middepth(108.5) surface(58.1) bottom(9.3): smallest
Ebb: ns
3. Tide × station
Flood; largest: east(158.6) west(110.1) channel(58.6): smallest
Ebb: ns

*Significant at $\alpha = 0.05$.
[1]ns—no significant difference(s).

APPENDIX TABLE 2.—Three-way analysis of variance for Atlantic croaker, *Micropogonias undulatus*, postlarvae captured at buoy 32, 14-15 March 1978. Catch data are $\log_{10}(10 + X)$ transformed.

Source	df	SS	MS	F	Source	df	SS	MS	F
Photoperiod, P	1	0.0594	0.0594	1.46	P × S	6	2.1754	0.3626	8.91*
Tide, T	1	0.1086	0.1086	2.67	T × S	6	0.6195	0.1033	2.54*
Sites, S	6	9.3385	1.5564	38.24*	P × T × S	6	0.5752	0.0959	2.36
P × T	1	0.5152	0.5152	12.66*	Error	24	0.9769	0.0407	

Multiple comparisons (Numbers in parentheses are mean catch for each stratum.)

A. Photoperiod × tide (Bonferroni *t*-tests; $\alpha = 0.05$)
   Largest: flood/night(301.4) ebb/day(249.7) flood/day(266.6) ebb/night(143.5): smallest

B. Sites (Bonferroni *t*-tests; $\alpha = 0.05$)
   1. Depths: east and west
      Bottom (311.6)>surface (69.5)
   2. Depths: channel
      Largest: middepth(636.6) bottom(193.2) surface(28.1): smallest
   3. Stations: ns[1]

C. Photoperiod × site (Bonferroni *t*-tests; $\alpha = 0.05$)
   1. Photoperiod × depth: east and west
      Day: bottom(404.6)>surface(25.7)
      Night: bottom(218.5)>surface(107.0)
   2. Photoperiod × depth: channel
      Day; largest: middepth(590.9) bottom(288.7) surface(6.3): smallest
      Night; largest: middepth(682.2) bottom(65.9) surface(57.2): smallest
   3. Photoperiod × station
      Day: ns
      Night: ns

D. Tide × site (Bonferroni *t*-tests; $\alpha = 0.05$)
   1. Tide × depth: east and west
      Flood: bottom(336.3)>surface(110.7)
      Ebb: bottom(286.8)>surface(38.7)
   2. Tide × depth: channel
      Flood; largest: middepth(865.7) bottom(110.0) surface(31.6): smallest
      Ebb; largest: middepth(407.4) bottom(304.2) surface(23.6): smallest
   3. Tide × station
      Flood; largest: east(336.8) channel(335.8) west(110.1)
      Ebb: ns

*Significant at $\alpha = 0.05$.
[1]ns—no significant difference(s).

APPENDIX TABLE 3.—Three-way analysis of variance for *Paralichthys* spp. postlarvae captured at buoy 32, 14-15 March 1978. Catch data are $\log_{10}(10 + X)$ transformed.

Source	df	SS	MS	*F*	Source	df	SS	MS	*F*
Photoperiod, P	1	0.3217	0.3217	12.55*	P × S	6	1.7818	0.2970	11.58*
Tide, T	1	2.5208	2.5208	98.32*	T × S	6	1.1400	0.1900	7.41*
Sites, S	6	1.8388	0.3065	11.95*	P × T × S	6	0.4869	0.0812	3.17*
P × T	1	0.2309	0.2309	9.00*	Error	24	0.6154	0.0256	

Multiple comparisons (Numbers in parentheses are mean catch for each stratum.)

A. Photoperiod
Night (50.3) >day (45.7)

B. Tide
Flood(84.7) >ebb(11.1)

C. Sites (Bonferroni *t*-tests; $\alpha = 0.05$)
1. Depths: east and west; bottom (62.3) >surface (37.8)
2. Depths: channel
Largest: middepth(89.8) surface(20.3) bottom(14.9): smallest
3. Stations largest: east(79.3) channel(41.6) west(20.8): smallest

D. Photoperiod × tide (Bonferroni *t*-tests; $\alpha = 0.05$)
Largest: flood/night(87.0) flood/day(82.3) ebb/night (10.5) ebb/day(11.6): smallest

E. Photoperiod × site (Bonferroni *t*-tests; $\alpha = 0.05$)
1. Photoperiod × depth: east and west
Day: bottom(89.0) >surface(3.4)
Night: ns[1]
2. Photoperiod × depth: channel
Day; largest: middepth(103.4) bottom(19.1) surface(1.9): smallest
Night; largest: middepth(76.1) surface(44.8) bottom(9.2): smallest
3. Photoperiod × station
Day: ns
Night; ns

F. Tide × site (Bonferroni *t*-tests; $\alpha = 0.05$)
1. Tide × depth: east and west
Flood: ns
Ebb: ns
2. Tide × depth: channel
Flood; largest: middepth(156.4) surface(29.4) bottom(12.4): smallest
Ebb: ns
3. Tide × station
Flood; largest: east(160.3) channel(66.1) west(35.5): smallest
Ebb: ns

*Significant at $\alpha = 0.05$.
[1]ns—no significant difference(s).

RELATIONSHIPS BETWEEN WAVE DISTURBANCE AND ZONATION OF BENTHIC INVERTEBRATE COMMUNITIES ALONG A SUBTIDAL HIGH-ENERGY BEACH IN MONTEREY BAY, CALIFORNIA

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ABSTRACT

Benthic marine invertebrate communities were organized along a gradient of wave-induced substrate motion on the subtidal high-energy beach in Monterey Bay, California. Two general zones were distinguished from 6 to 30 m of water. A shallow zone (<14 m) contained sediments that were commonly disrupted by wave activity and it was primarily occupied by small, mobile, deposit-feeding peracarid and ostracod crustaceans. Patterns of crustacean morphology and mobility were related to their depth zonation. Few animals lived in permanent tubes or burrows in the crustacean zone. Wave disturbance decreased with increasing water depth, while the numbers of sessile and semisessile species, commensal animals, and suspension or selective-surface-deposit feeders increased. The deeper zone (>14 m) was dominated by polychaete worms living in relatively permanent tubes and burrows. A variety of descriptive-correlative evidence indicates that community zonation is strongly influenced by wave-induced bottom disturbance. The evidence includes: 1) a positive correlation between water depth and the numbers of tube dwellers, burrow dwellers, and commensal animals which apparently cannot establish or maintain populations in shifting sediments; 2) other depth and thus substrate disturbance related natural history patterns; 3) a positive correlation between the strength of wave activity and the width and depth limits of the faunal zones (i.e., when wave disturbance is more intense, the crustacean zone ends and the polychaete zone begins in deeper water); 4) a correspondence between the largest decrease in polychaete population size and the season and location of greatest wave activity (winter months at the shallowest station); and 5) a marked similarity between community zonation along a depth-dependent gradient of oscillatory substrate motion (gently sloping sandflats) and the zonation along a constant depth gradient of creeping substrate motion (submarine canyon ridge). Other explanations are inconsistent with these biological patterns and, thus, wave disturbance is apparently the major physical process affecting community zonation.

Sedimentary environments are dynamic and strongly influenced by water currents and the physical and biological properties of the sediment. These animal-sediment relations have become a major focus of benthic community studies since the pioneering work of Sanders (1958, 1960) and Rhoads and Young (1970) and were recently reviewed by Rhoads (1974) and Gray (1974). This previous work was primarily restricted to wave-protected embayments where deposition and resuspension of fine sediments is a major process. In contrast, the open-coastal environment is commonly subjected to oceanic swell which has a dramatic effect on substrate motion (e.g., Komar 1976). Although sediment scour and motion are major sedimentary processes affecting the shallow parts of most continental shelves, little is known about their effect on the establishment and maintenance of soft-bottom communities.

The large areal scale of gradients in wave-induced bottom disturbance and the corresponding community patterns are difficult to manipulate experimentally. However, potential relationships between wave disturbance and community zonation can be explored by a posteriori correlations and by a priori use of "natural experiments" (sensu Cody 1974). While communities are often organized along gradients of environmental variability (Whittaker 1962, 1967; Mills 1969; Nichols 1970), the complex interactions between physical and biological regulatory processes are rarely understood. The descriptive and experimental studies in the marine rocky intertidal habitat are an important exception (e.g., Connell 1961; Dayton 1971; Ricketts et al. 1972; Stephenson and Stephenson 1972; Paine 1974; Lubchenco and Menge 1978). This study has two primary objectives: to describe the zonation of benthic inverte-

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brates along a subtidal high-energy beach; and to examine the relationship between community zonation and wave-induced bottom disturbance. Understanding the role of this predominant physical process is critical to subsequent studies of biological phenomena and their interactions with the physical sedimentary environment.

METHODS

The study area was in central Monterey Bay, Calif., on the sandflats adjacent to the Monterey Submarine Canyon and along a ridge in the canyon head (Figure 1). The southern sandflat transect was the main study site (Figures 1, 2). Stations in 6 (M-1), 9 (M-2), 14 (M-3), 18 (M-4), and 24 m (M-5) of water were sampled at approximately the same time from June 1971 to June 1974. Three stations (9, 18, 24 m) were sampled along the northern sandflat from August 1974 to June 1975 (Figure 1; N stations). The maximum interval between sampling periods was 3 mo. Therefore, samples were taken during at least the four major seasons at each station. The two deepest stations along the northern sandflat (N-5, 30 m; N-6, 40 m) were only sampled in May 1975. Samples were treated separately to document seasonal patterns and were combined over the study period for each station to examine general zonal patterns.

A third, but much shorter transect (40 m long) was located along a flat ridge in the head of the Monterey Submarine Canyon (Figure 1). Four stations were established at 10 m intervals and at a constant water depth of 14 m. One end of the transect (station D) was highly disturbed by the slumping of sediment down an adjacent terrace wall. No sediment slumping occurred along the opposite end of the transect (station A) (see Environmental Setting section). The movement of sediment by slumping was measured by periodic depth soundings along the terrace wall and by diver observations and measurements at permanent underwater stations. Divers measured the distance from the bottom to the tops of the steel station rods at monthly intervals from May to November 1972. Periodic visual observations of station migrations and algal accumulations proceeded until mid-1974.

All samples and field observations were made by divers using scuba. Routine samples were taken with diver-held can corers (length = 17 cm; area = 0.018 m²) and were washed over a 0.5 mm screen in the laboratory. Eight replicate can cores were usually taken in a haphazard fashion (Fager 1968) at each station on each sampling date. The can corers were 3-lb coffee cans with both ends removed. Animal and sediment loss were prevented by water-tight snap-on plastic lids. Residues were fixed in 4% formaldehyde and transferred to 70% ethanol after sorting. The macrofaunal invertebrates were identified to species (i.e., nematodes, foraminiferans, and copepods were excluded).

A long, diver-operated corer (length = 60 cm; area = 0.018 m²) was used to document the vertical distribution of organisms within the sediment at southern sandflat stations in 9, 18, and 30 m of water during August 1972. To maintain the strata and minimize animal movement through them, the corers were held horizontally after sample procurement. Some cores were sectioned immediately in the boat and others were sectioned within an

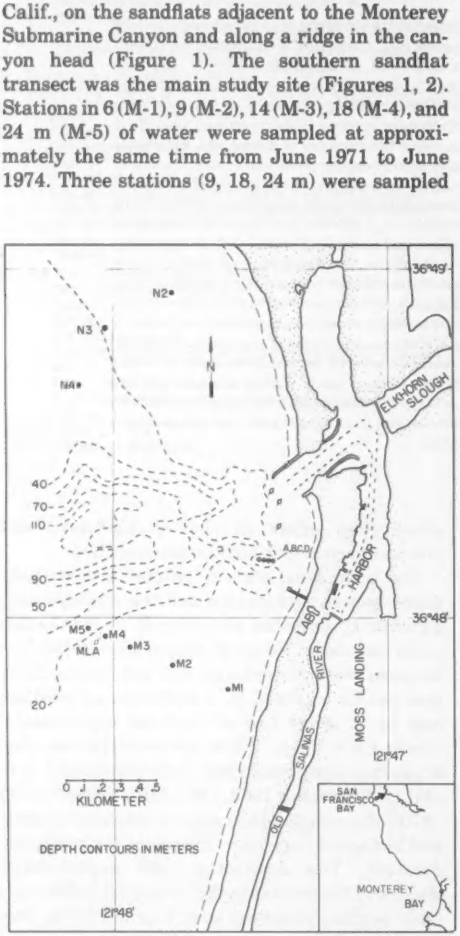

FIGURE 1.—Southern (M) and northern (N) sandflat stations and the canyon transect (A-D) in central Monterey Bay, Calif. N-5 and N-6 were directly east of N-4, 0.5 and 1 km, respectively.

hour at the laboratory. Biomass was calculated from samples taken with a hydraulic suction dredge (Brett 1964) in August 1972. Vertical layers were excavated from a 0.25 m^2 cylinder and collected separately in 1 mm mesh bags. Animals were weighed after being removed from 70% ethanol and air-dried for 10 min. These weights were converted to grams of organic material with the conversion factors of Lie (1968).

Animals swimming near the bottom were sampled with a funnel trap, an inverted funnel (20 cm in diameter) with the spout leading up and into a holding jar. Legs held the traps within several centimeters of the bottom. These traps were set periodically throughout the entire year, primarily at M-2 (Figure 1; 9 m).

The availability of polychaete larvae was estimated by the settlement of larvae into plastic collecting jars. The jars were wide-mouth gallon containers (mouth diameter = 10.5 cm; volume = 4.5 l) held vertically in a rack at a height of 1 m from the bottom. Jars were collected at 14-day intervals from September 1972 to June 1975 at station M-4 (Figure 1; 18 m). No sediment was placed in the jars, but a 1 or 2 cm layer of seston accumulated during each interval. The jars were covered with a galvanized mesh (1 cm square) to prevent the entrance of fish. The jar contents were washed over a 0.25 mm screen and preserved in 4% formaldehyde. Postsettlement polychaetes were identified to species.

Diver observations of sediment movements and current patterns were frequent. Direct measurements of wave height and wave period were also made in the northern bay from September 1971 to February 1973. They were recorded by the Corps of Engineers from Santa Cruz Pier approximately 18 km from the study area. Although wave heights were generally greater in the central bay, the seasonal patterns were similar throughout the bay.

Feeding and burrowing observations were made in the laboratory and gut contents were examined under a compound microscope. If an animal contained only sediment, it was called a deposit feeder. Some deposit feeders also preyed on other infauna in an aquarium.

ENVIRONMENTAL SETTING

Central Monterey Bay is characterized by high-energy beaches (sensu Clifton et al. 1971) that have a relatively gentle seaward slope and a well-developed winter berm. The most distinct physiographic feature is the large Monterey Submarine Canyon (Figure 1). Prevailing wind and wave direction is from the northwest. Wave refraction in relation to bottom topography concentrates wave energy on the northern sandflat and disperses wave energy in the canyon head and along a portion of the adjacent southern sandflat. Width of the breaker zone and wave height increase dramatically to the north and south of the canyon head (Gordon 1974).

Wave-generated bottom currents have primary control over the sedimentary environment of a beach. Clifton et al. (1971) gave a detailed description of wave-generated depositional structures in the high energy-nearshore environment along the southern coast of Oregon. The same major depositional structures and zones were present in central Monterey Bay. The relative position of the nearshore and offshore is illustrated in Figure 2. The bulk of the faunal sampling and other field observations was performed in the offshore area (Figure 2).

Strong longshore tidal currents can produce lingoid and undulatory small ripples (Reineck and Singh 1973) that trend perpendicular to the ripples produced by oscillating wave-generated currents. Both types were observed at the stations in 18 m of water and deeper, and often resulted in a complicated maze of discontinuous ripple crests. In shallower water, wave-generated currents were more intense and dominated the depositional structure. They produced ripple crests in the fine sand that were more or less continuous and normal to the direction of wave arrival. During periods of large winter swell, conditions at the 9 m station were very similar to those described for the "outer planner facies" of the nearshore by Clifton et al. (1971). Here, ripple marks were obliterated by wave currents and the sediment moved in sheet flow. Fager (1968) observed similar "miniature sandstorms" on the sandflats adjacent to the Scripps Institution of Oceanography in southern California.

The bottom threshold velocity of sediment movement is highly dependent on water depth. Given the narrow range of grain size distributions among the sandflat stations (Table 1), the predominant factors controlling the threshold of sediment movement along the sandflat transects were undoubtedly water depth, wave height, and wave period (Komar 1976). Since unidirectional longshore currents had a decreasing impact on the surface sedimentary structures with decreasing

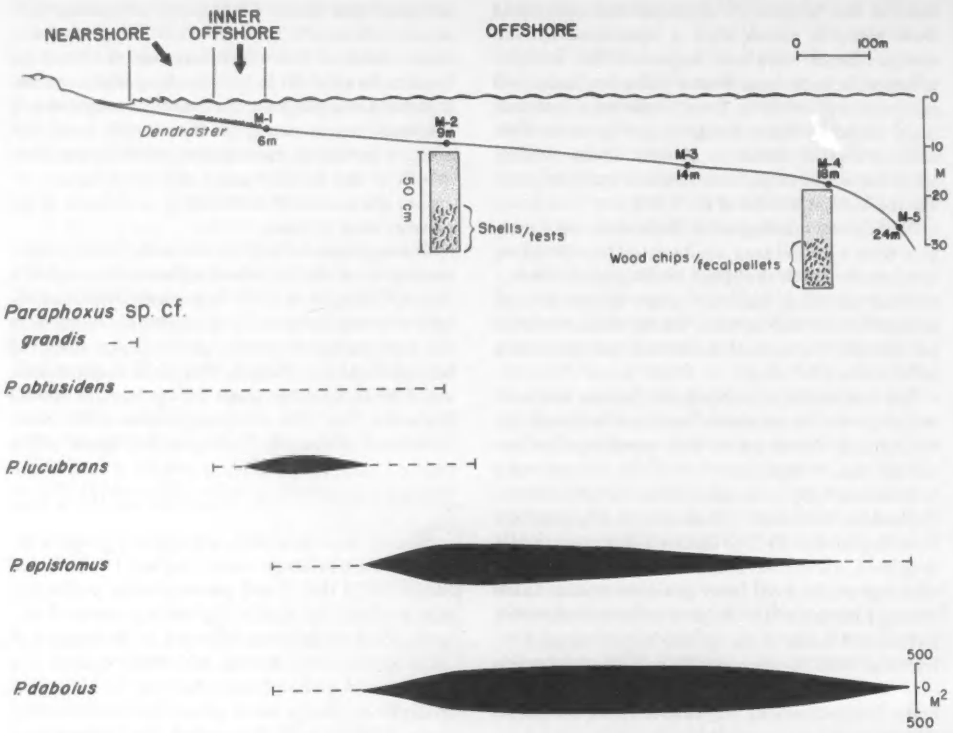

FIGURE 2.—Schematic profile of the beach along the southern transect showing sediment profiles from long cores and the zonation of paraphoxid amphipods in Monterey Bay, Calif.

TABLE 1.—Characteristics of the surface sediments along southern (M) and northern (N) transects in Monterey Bay, Calif. (mean ± 95% confidence limits).

Station	Depth (m)	*n* samples	Md (ϕ)[1]	% fine sand (0.250-0.062 mm)	% silt (<0.062 mm)	Coefficient sorting[2]	% organic carbon
M-1	6	6	2.93±0.30	94.4± 5.4	1.0±1.3	0.44±0.03	0.08±0.012
M-2	9	11	3.27±0.04	91.4± 3.6	8.1±3.8	0.47±0.04	0.13±0.020
M-4	18	7	3.39±0.05	93.3± 1.5	6.2±1.5	0.38±0.02	0.10±0.050
M-5	24	7	3.53±0.05	87.6± 2.0	10.8±1.6	0.43±0.02	0.18±0.020
N-2	9	3	3.04±0.20	96.1± 7.0	1.0±0.1	0.42±0.20	—
N-3	18	3	3.15±0.03	95.5± 3.6	1.3±1.9	0.42±0.03	—
N-4	24	3	3.06±0.10	88.9±14.0	2.0±0.3	0.54±0.30	—

[1] ϕ = −log (median diameter).
[2] Folk and Ward (1957); higher coefficient equals poorer sorting.

water depth, the primary sediment movements were caused by waves intercepting a shoaling bottom.

An increase in wave height and a decrease in wave period both cause an increase in the velocity of sediment movement (Komar 1976). As a result, winter wave conditions should cause the greatest sediment motion (Figure 3). Hundreds of dives and years of qualitative observations of wave activity indicated a strong gradient in substrate movement with changing depth along the sandflats as well as considerably greater sediment motion dur-

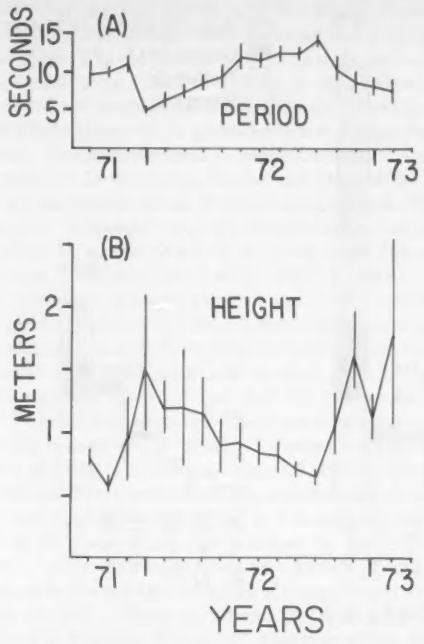

FIGURE 3.—Monthly wave periods (A) and heights (B) during 1971-73 at the Santa Cruz pier in northern Monterey Bay, Calif. (means and ranges).

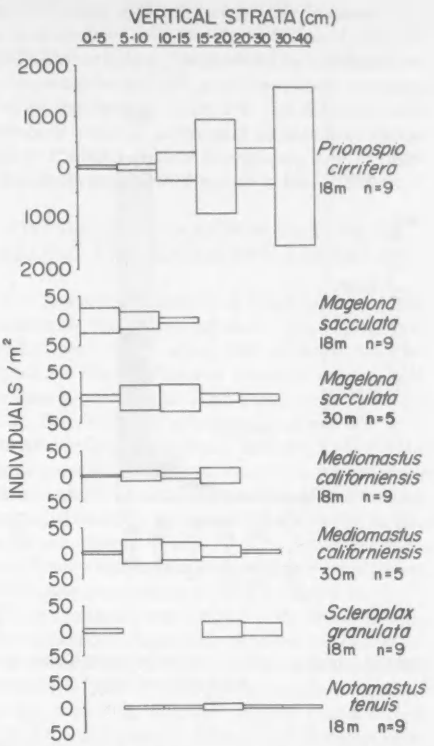

FIGURE 4.—Vertical distribution of invertebrate species living deep in the sediment in Monterey Bay, Calif. (mean per layer based on n cores 50 cm long).

ing the late fall and winter months. These observations are consistent with theoretical expectations (Komar 1976).

Examination of the residue retained by the 0.5 mm mesh screen during the processing of vertical strata from the long cores revealed additional characteristics of the depositional environment. At the 9 m station, strata below 25 cm contained broken tests and spines of the sand dollar *Dendraster excentricus*, broken mollusc shells, and rounded, olive-green silt stones. The surface stratum (top 25 cm) was homogenous fine sand (Figure 2). Similar stratification was observed by Howard and Reineck (1972) in the upper offshore of a low-energy beach along Sapelo Island, Ga. This concentration of shells and tests probably resulted from physical winnowing or reworking during severe storms.

Long cores from 18 and 30 m had no shell/test strata. Instead, there was a concentration of woody chips of terrigenous, riverine origin and a high density of large oblong fecal pellets (1 mm length) below 25-30 cm in the sediment (Figure 2). The fecal pellets belonged to the deposit-feeding capitellid polychaete *Notomastus tenuis*, which lives deep in the sediment column (Figure 4). Although fecal pellets were produced in situ, the wood chips had been deposited on the surface and were either buried by subsequent deposition or by the biological reworking of the upper sediment layers. Many large deposit feeders burrowed to a depth of 20-30 cm (Figures 4, 5, 6). Nevertheless, this deposit would not persist at the shallower depths of stronger physical winnowing.

In summary, surface ripple mark patterns, the composition of deep sediment layers, frequent field observations, and theoretical predictions indicate a unidirectional gradient in substrate motion highly dependent on depth.

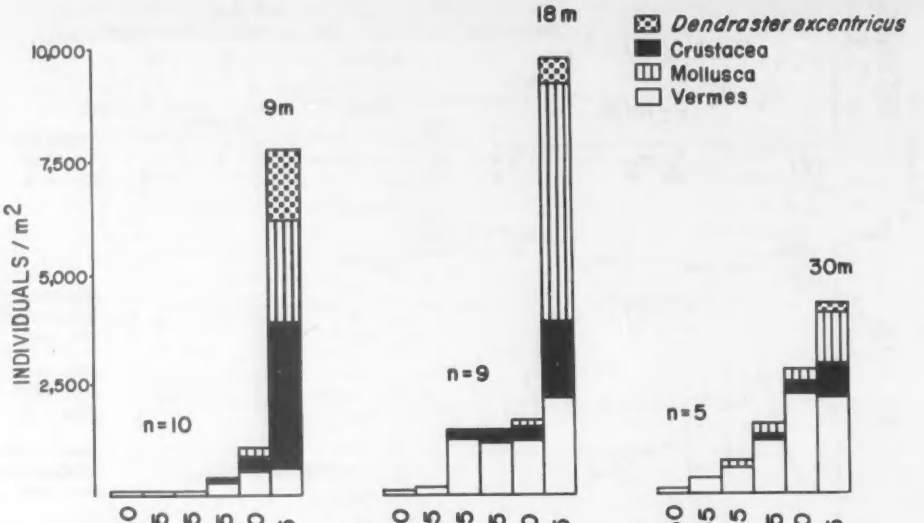

FIGURE 5.—Mean number of individuals per square meter per long core layer in n long cores in Monterey Bay, Calif. Vermes are 90% polychaetes and include enteropneusts, phoronids, oligochaetes, and nemerteans.

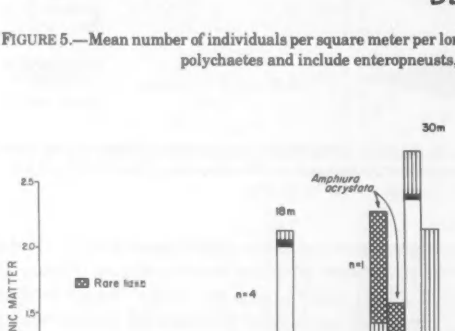

FIGURE 6.—Mean biomass of animals per suction dredge layer in Monterey Bay, Calif. (except at 30 m, where n = 1). Rare taxa indicated. See Figure 5 for bar legend.

Sediment movements in the canyon head included unidirectional down-canyon creeping and slumping as well as oscillatory movements. Diver observations and measurements at permanent bottom stations indicated a general shoaling of shallow (5-15 m) terrace walls and an accumulation of drift plants (primarily *Ulva lobata, Macrocystis pyrifera, Zostera marina*) during the summer and early fall. Slumping of terrace walls and down-canyon flushing of channels were coincident with the first fall storms and continued through the winter (see Arnal et al. 1973). The same seasonal cycle of sediment accumulation and flushing was observed at the heads of the Scripps and La Jolla Submarine Canyons (Shepard and Dill 1966).

One of the major slumping events occurred at the shoreward end of the flat canyon ridge. Sediment creeped down the terrace wall (5-14 m), across the ridge (14 m), and into the deeper canyon channel (25 m). The slumping was evidenced by a change in the position of the terrace wall, the exposure of consolidated mud outcrops on the ter-

race after the fall storms, and the down-canyon movements of station markers along this part of the ridge. The change in the terrace wall position was reflected in a 1 or 2 m increase in the depth of a midwall reference station and in the shifting of the wall base closer to the permanent stations on the ridge. The station markers (rods) at station C and especially D were also moved and slanted in a down-canyon direction. Furthermore, a large ship anchor, dropped in slightly deeper water below station D, moved about 10 m in the same down-canyon direction (Arnal et al. 1973). In contrast, the station stakes at stations A and B remained in a vertical position and did not move. The slumping of the terrace wall during the fall and winter was observed in other years and in other parts of the canyon head as well (Arnal et al. 1973; pers. obs.).

The four ridge stations (A-D) were established along a gradient of substrate motion. Station D was nearest to the slump zone and station A was farthest from the terrace wall, where there was no evidence of sediment slumping. The animals were sampled once along the transect in December 1972. Although there were no significant differences in the median diameter of the sediment and the sorting coefficients among the four stations ($P>0.1$; Kruskal-Wallis test, Conover 1971), the surface sedimentary structures indicated the persistence of the substrate disturbance gradient from October to December. During this entire period, the sandy sediment was well consolidated and formed parallel ripple marks at stations A and B, but was poorly consolidated and had no ripple marks at stations C and especially D (the area of creeping).

This change in substrate consolidation and ripple mark patterns was not caused by changes in tidal or oscillatory-wave currents. Tidal and longshore currents did not vary along the 40 m transect. Moreover, since oscillatory bottom currents primarily depend on the grain size, water depth, wave height, and wave period (Komar 1976), which were all constant along the transect, the bottom threshold of sediment movement by these currents did not differ among the ridge stations. Therefore, the slumping gradient cannot be quantified in terms of resuspended material or bottom current velocity. On the other hand, poorly consolidated sandy sediments characterized all the slump areas we observed in the canyon head and were also documented in a large slump near the Scripps Canyon in southern California (Van-Blaricom 1978; pers. obs.). These slumping events are extremely difficult to quantify because they have never been witnessed (see Shepard and Dill 1966). Nevertheless, the observations and indirect measurements indicate a unidirectional gradient of substrate motion related to the distance from slumping canyon walls and channeling topography. Stations A (low movement) and D (high movement) represent the ends of this gradient.

OFFSHORE ZONATION PATTERNS ALONG THE SOUTHERN SANDFLAT

The gradational nature of the invertebrate assemblages was apparent from the changes in species abundance along the offshore transect (Table 2). The crustaceans were the numerically dominant group at the 6 and 9 m stations (M-1 and M-2). The density of crustacean species and individuals was highest at 9 m (Figures 7, 8). Six of the seven most abundant species at this station were crustaceans (Table 2). The number of crustaceans decreased steadily seaward of 9 m. The 14 m station was a distinct transition zone between a shallow offshore crustacean assemblage and a deeper polychaete assemblage (Table 2; Figure 7).

The 6 m station was located at the seaward edge of a large bed of *Dendraster excentricus*. The width of the sand dollar bed increased with distance from the canyon head. It was approximately 40 m at the southern sandflat transect (Figure 1) and >75 m wide 2 km to the south. Merrill and Hobson (1970) described a protected open coast *D. excentricus* bed which was similar to the local situation.

Crustacean Zone

Crustaceans

The abundant animals of the shallow-water zone were small, actively burrowing, deposit-feeding amphipods and ostracods (Table 2). The amphipods belonged to three typically sand-dwelling families, Oedicerotidae, Phoxocephalidae, and Haustoriidae, and the ostracods to the Philomedidae. Each family was represented mainly or exclusively by one genus of several species and each species was often found within distinct depth limits.

The genus *Eohaustorius* contained the only representatives of the subfamily Haustoriinae on this coast (Bousfield 1970). Temporal variations in *Eohaustorius sencillus* and *E. sawyeri* were relatively complementary at the 6 m station and may

TABLE 2.—Ten most abundant species at each station along southern transect in Monterey Bay, Calif. Data are number/square meter ± 95% confidence limits and percent frequency of occurrence in *n* samples in parentheses. × = species that ranked 11-17 in abundance; B = semipermanent burrow; T = tube dweller.

	Crustacean zone			Polychaete zone	
Species	M-1, 6 m *n* = 108	M-2, 9 m *n* = 107	M-3, 14 m *n* = 30	M-4, 18 m *n* = 141	M-5, 24 m *n* = 28
Crustacea:					
Euphilomedes longiseta	854±209 (81)	397±110 (52)			
Eohaustorius sencillus	351±105 (60)	1,234±165 (100)	333±127 (80)		
Paraphoxus lucubrans	298± 72 (68)				
E. sawyeri	182± 50 (58)				
Synchelidium spp.	143± 44 (59)				
P. obtusidens	66± 21 (31)				
Euphilomedes oblonga		1,064±204 (87)	513±220 (93)	×	
P. daboius		799±176 (94)	970±209 (100)	402± 61 (91)	×
P. epistomus		722±116 (98)	320± 94 (97)		
E. carcharodonta		397±116 (76)	×	×	
Mollusca:					
Clivella pycna	309±479 (37)				
Tellina modesta	55± 17 (43)	738±162 (93)	132± 61 (63)	722±171 (68)	309±121 (93)
Mysella aleutica		386±110 (81)	×		
Protothaca staminea			×	105± 39 (44)	×
Polychaeta:					
Prionospio pygmaea T, B	110± 50 (19)	×	149± 72 (60)	237± 50 (84)	573±342 (68)
Scoloplos armiger	105± 33 (56)				
Armandia bioculata		276±133 (32)			
Magelona sacculata B	×	237± 72 (61)	303±171 (80)	1,174±231 (94)	626±220 (100)
Amaeana occidentalis B		×	204± 72 (87)	138± 39 (57)	276±110 (68)
Mediomastus californiensis		×	182± 66 (80)	331± 50 (93)	1,053±231 (96)
Northria elegans T		×	116± 44 (67)	242± 28 (96)	435± 94 (100)
Lumbrineris luti B				226± 28 (94)	242± 50 (93)
P. cirrifera T, B				193± 99 (55)	303±132 (59)
Nephtys cornuta				×	325±105 (93)
Edwardsia sp. (Anthozoa) B				×	150± 62 (80)

indicate a well-defined boundary between the two populations (Figure 9). No *Eohaustorius* were captured in funnel traps, indicating that much of the life history occurs on or within the sediment.

The genus *Paraphoxus*, in contrast to *Eohaustorius*, has a wide depth distribution in Monterey Bay (Barnard 1960). Four species occurred along the subtidal transect in much greater densities than populations from deeper portions of the bay (Barnard 1960; Hodgson and Nybakken 1973) and in more well-defined zones (Figure 2). A fifth species was the intertidal *Paraphoxus* sp. cf. *grandis*, a new species (Slattery in prep.).

There is an obvious relationship between certain morphological characteristics and the depth zonation of *Paraphoxus* spp. Larger species reached their peak abundance in shallower water (Table 3). *Paraphoxus* sp. cf. *grandis* and *P. obtusidens* were giants relative to the other three species (Table 3). This large size may be an adaptation to strong sediment motion (Sameoto 1969; Fincham 1971). In contrast, *P. epistomus* and *P. lucubrans* were more streamlined and slightly larger than the deepest species, *P. daboius*. *Paraphoxus daboius* was small and had poorly developed eyes (Table 3). It lived in the calmest water (i.e., deepest) and finest sediment and was the only peracaridean crustacean commonly found below 5 cm in the long cores. *Paraphoxus* were captured by the funnel traps (Table 4).

Euphilomedid ostracods were among the most abundant crustaceans (Table 2). They occasionally occurred in funnel traps (Table 4). In contrast, cumaceans were not abundant on the bottom (Table 2), but were numerous in funnel traps (Table 4). A number of other rare bottom dwellers were also abundant in the funnel traps, including the oedicerotid amphipods *Synchelidium shoemakeri, Synchelidium* spp., and *Monoculodes spinipes*; other amphipods *Atylus tridens, Tiron biocellata*, and *Megaluropus longimerus*; and a number of mysids (Table 4).

No general correlation exists between swimming tendency and species zonation within the crustacean zone. Although more active *Paraphoxus* species were found in shallow water, nonswimming *Eohaustorius* spp. lived at the same depths. Moreover, the cumaceans and oedicerotid amphipods were active swimmers (Table 4) and occurred in relatively low numbers throughout the crustacean zone. On the other hand, there were distinct morphological patterns suggesting greater swimming among shallower species within particular groups (i.e., *Paraphoxus* and *Euphilomedes* species); however, these groups and others may enter the water column for very differ-

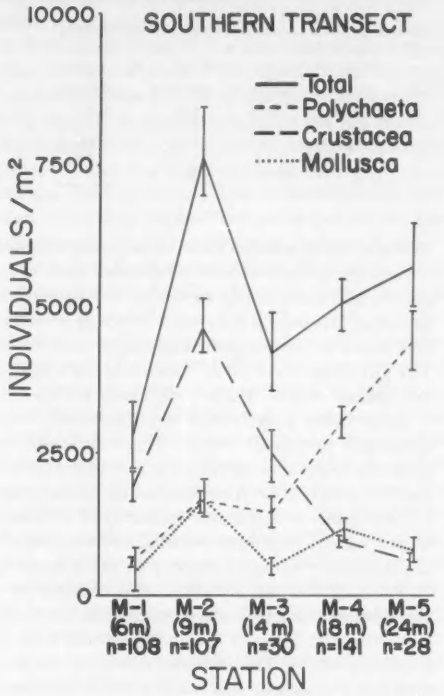

FIGURE 7.—Mean number of individuals per square meter and 95% confidence limits of major groups along the southern transect in Monterey Bay, Calif. (estimates based on n can cores).

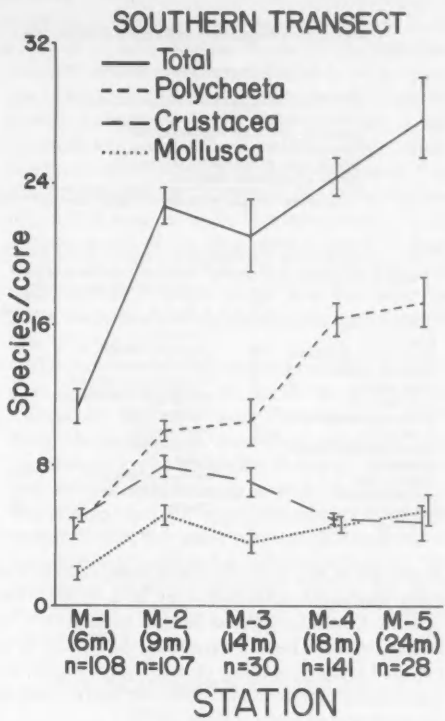

FIGURE 8.—Mean number of species per can core (0.018 m²) and 95% confidence limits of major groups along the southern transect in Monterey Bay, Calif.

ent reasons (e.g., mating, food, substrate movements). Despite these differences, almost all the crustaceans in the crustacean zone were active, free-burrowing species and few inhabited tubes.

Other Animal Groups

The polychaetes were much less abundant than crustaceans in the crustacean zone (Table 2; Figure 7). *Scoloplos armiger*, *Chaetozone setosa*, *Nephtys caecoides*, and *Dispio uncinata* were the most characteristic species at the shallowest station (M-1). *Prionospio pygmaea* and *Magelona sacculata* maintained highly ephemeral populations near the surf zone (see Seasonal Patterns). The uncommon onuphid *Onuphus eremita* was only encountered at 6 m (M-1). In general, the more frequent members of the polychaete as-

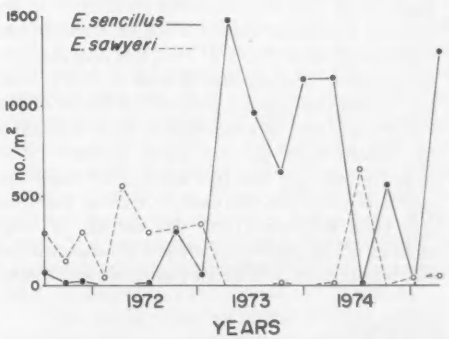

FIGURE 9.—Complementary temporal variations of *Eohaustorius sencillus* and *E. sawyeri* at M-1 (6 m) in Monterey Bay, Calif.

TABLE 3.—Gradation of adult morphological characters in the five species of paraphoxid amphipods in Monterey Bay, Calif.

Character	*Paraphoxus* sp. cf. *grandis*	*P. obtusidens*	*P. lucubrans*	*P. epistomus*	*P. daboius*
Depth of dispersion center	Intertidal	<6 m	≥6 m	9 m	14 m
Mean size (mm) mature females (±SD)	15±2.5	12±2.2	4.5±0.8	3.7±0.4	2.8±0.2
Ratio of eye diameter to body length	1:35	1:39	1:17	1:33	1:56
Ratio of inner[1] to outer ramus of uropod III	1:1.09	1:1.04	1:1.1	1:1.5	1:4.2
Number of individuals measured	10	10	20	20	20

[1]Higher ratio indicates more foliose uropod used in swimming.

TABLE 4.—Abundance of crustaceans caught in funnel traps at station M-2 (9 m) in Monterey Bay, Calif. (410 trap days).

Species	No. trapped	Species	No. trapped
Amphipods:		Cumaceans:	
Synchelidium shoemakeri	160	*Diastylopsis tenuis*	57
Paraphoxus daboius	79	*Lamprops carinata*	35
Atylus tridens	66	*Hemilamprops californica*	27
Tiron biocellata	40	*Mesolamprops bodegensis*	25
Monoculodes spinipes	40	*Cyclaspsis* spp.	9
P. epistomus	11	*Anchicolorous occidentalis*	4
Megaluropus longimerus	1	Mysids:	
Ostracods:		*Neomysis kadiakensis*	550
Euphilomedes carcharodonta	12	*Acanthomysis* spp.	250
E. longiseta	7	Others	50
E. oblonga	5		

semblage at M-1 were mobile deposit feeders. The most abundant polychaetes at M-2 (9 m) were species that maintained larger populations in deeper water. The one exception, *Armandia brevis*, had a low frequency of occurrence (Table 2), was highly opportunistic, and primarily lived in more protected areas (Oliver 1979).

Polychaete Zone

The polychaete zone (Table 2) was characterized by animals that require a more stable substratum to establish and maintain burrows and tubes. Most of the polychaetes living exclusively in the shallow crustacean zone did not have permanent tubes or burrows (Table 2). This was true of all the crustaceans. The gradual change in ripple mark and vertical sedimentary structure discussed previously reflected this increase in substrate stability. There were several other distinct visual changes between the two zones. The most conspicuous were the increase in burrow openings and tube fragments and the density of large siphons of the goeduck, *Panopea generosa*, which was first encountered in the transition area (14 m).

Polychaetes

The polychaetes *Magelona sacculata* and *Nothria elegans* were abundant at the deeper stations (Table 2). The onuphid *N. elegans* lived in a vertical tube constructed of clean sand. Laboratory observations and gut contents indicated that *N. elegans* was a surface-deposit feeder, scavenger, and predator. *Magelona sacculata* lived in a burrow and was a surface-deposit and suspension feeder. The gut contents of 25 *M. sacculata* were mainly amorphous organic matter with very little sand.

Many other polychaetes were generally more abundant in deeper water. These included the spionids *Prionospio cirrifera* and *P. pygmaea* and the large terebellid *Amaeana occidentalis* (Table 2). *Amaeana occidentalis* constructed a burrow with a mucus-impregnated wall and was capable of extensive burrowing activity in the laboratory. The mouth was often positioned a centimeter or more below the substrate surface with the tentacles extended through the sediment and into the overlying water. The gut contents of *A. occidentalis* and *Prionospio* spp. were similar to those of *M. sacculata*. Apparently, they scrape fine material from the sediment-water interface and catch suspended particles.

In general, a higher proportion of animals was found in lower vertical sediment strata from the polychaete zone (>14 m depth) compared with the crustacean zone (Figures 5, 6). This was expected due to the greater number of tube- and burrow-dwelling inhabitants. Coincident with this increase was an increase in known or suspected commensal or symbiont animals. These included the pinnotherid crabs *Scleroplax granulata* (Figure 4) and *Pinnixa franciscana* and several species of polynoid polychaetes. Although Day (1967) described the paraonid polychaetes as shallow surface burrowers, almost half of the individuals of the three local species (*Aricidea suecica, Aedicira pacifica*, and *Paraonides platybranchia*) were found below 10 cm in the sediment (9 individuals in 0-10 cm and 7 in 10-20 cm).

Several rather small species also burrowed deep into the sediment. The capitellid polychaete *Mediomastus californiensis* was generally <1 cm long after preservation and was found throughout the sediment column (Figure 4). Additionally, the

small (<1 cm long) *Prionospio cirrifera* was found as deep as 30-40 cm in the sediment (Figure 4). It was the most abundant polychaete from the long cores at the 18 m station (Figure 4) and yet ranked only seventh in abundance, when the top 10 cm of the sediment was considered separately. Spionids have ciliated feeding palps and dorsal gill filaments. They generally live in mucus-lined burrows or sand tubes and feed on, or just above, the bottom surface (Hartman 1941). Perhaps *P. cirrifera* inhabits the burrows of thalassinid shrimps in a manner similar to the phoronid worm *Phoronis pallida*. In Bodega Bay, Calif., *P. pallida* is found deep in the sediment in association with *Upogebia pugettensis* (Thompson 1972). The lower portion of the phoronid tube is constructed of relatively coarse sand and the distal end is composed of fine black sediment where the tube passes through the burrow wall of *U. pugettensis*. The tube is oriented normal to the shrimp burrow such that the lophophore can be extended into the burrow for feeding and respiration (Zimmer[2]). Coincidentally, the highest concentration of *P. cirrifera* per vertical stratum (175) was found deep (30-40 cm) in the only core that contained a large thalassinid, *Callianassa* sp.

It is important to note that these vertical patterns were not artifacts resulting from migration down the core or from physical disturbance. Corers were oriented horizontally while out of water and quickly cut by extruding the core from the corer bottom. Moreover, animals that were known to live very near to the sediment-water interface were not displaced (e.g., small bivalves, crustaceans, and *Nephtys cornuta*).

Other Animal Groups

Although the density of crustaceans was very low in the polychaete zone (Figure 7), the number of tube-dwelling forms was greater (e.g., *Ampelisca* and *Photis* species). Variations in the number of individuals and species of bivalve molluscs (Figures 7, 8) were due to periodical heavy settlement along the entire transect. Juvenile mortality was almost complete and very few specimens were observed that were larger than a few millimeters. The same observation was made by Muss (1973) in the Øresund in Denmark. The most abundant local bivalves were *Tellina modesta* and *Mysella aleutica* (Table 2). The distribution of *T. modesta* was correlated with the percentage of silt in shallow-water sediments by Barnard (1963). Large individuals were observed in the northern bay and in Moss Landing Harbor, where the fine sediment fraction was greater than that along the transects. There were also high numbers of small (1 mm) juvenile bivalves present in the surface strata of the long cores (Figure 5); however, most of the biomass of molluscs in the lower, hydraulically dredged strata was due to a few large individuals of *Solen sicarius* and *Macoma* spp. (Figure 6).

Ophiuroid communities are generally found at depths ranging from 45 to 90 m in southern California (Barnard and Ziesenhenne 1961). Large individuals of *Amphiura acrystata* were found deep in the substrate at the 24 m station. The animal's oral disc was usually 10-15 cm below the surface and its arms extended through the sediment into the water column. All observed individuals appeared to be suspension feeding. The density of *A. acrystata* was $<1/m^2$ at the 24 m station, but increased to 1 or $2/m^2$ south of the study area.

NORTHERN SANDFLAT

The northern sandflat received larger waves and the bottom surge was consistently greater than that along the southern sandflat. The theoretical difference in relative wave energy reaching both beaches was estimated from a detailed wave refraction diagram.[3] Assuming wave arrival from the northwest and wave period of 14 s, the total energy reaching the southern transect is only three-quarters of that arriving at a comparable segment of the northern beach. The southern stations also had finer sediment compared with the same northern depths (Table 1). During winter storms, wave heights in the northern area were often more than a meter higher than those at the southern study site. These differences only occurred close to the canyon in the vicinity of the sampling transects and were corroborated by hundreds of scuba diving observations of substrate motion and wave swell on the two sandflats.

If the primary control of the offshore zonation pattern is due to wave-induced substrate motion,

[2]R. Zimmer, Professor, Biology Department, University of Southern California, Los Angeles, CA 90007, pers. commun. June 1973.

[3]U.S. Army Corps of Engineers wave refraction diagrams 14-51-1, 1948.

then faunal zones should be shifted into deeper waters by an increase in wave activity. The difference in wave energy arriving at the two sides of the canyon allows a partial test of this hypothesis. As predicted, the animal zones described on the southern sandflat were wider and shifted toward deeper water on the northern sandflat (Figures 7, 10). Density of crustaceans was highest in 18 m of water, the transition zone was wider, and polychaetes did not increase in number until 30 m (Figure 10). Nevertheless, the shape of the curves in Figures 7 and 10, and thus the gross zonal patterns, were remarkably similar. The abundant species were the same on both sides of the canyon, but the rank orders of abundance were not identical (Oliver 1979). Abundance of the numerically dominant crustaceans and the total number of crustaceans was significantly higher along the northern transect (Figures 7, 10). Presumably, this increase was related to the extension of the crustacean zone into deeper water.

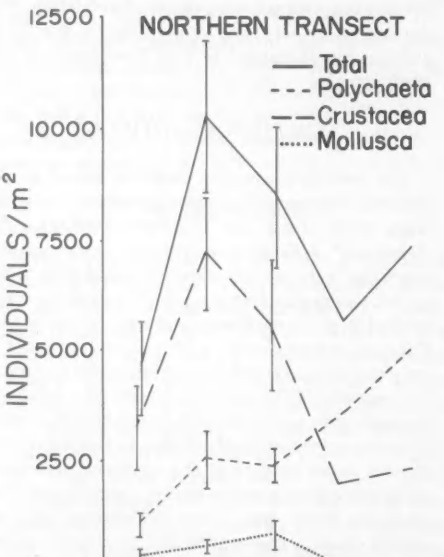

FIGURE 10.—Mean number of individuals per square meter and 95% confidence limits of major groups along northern transect in Monterey Bay, Calif. N-5 and N-6 were only visited once.

The predicted effect of increased wave activity on the infaunal zonation was also observed on the zonation of the sand dollar bed. During moderate to heavy sea states, the outer edge of the bed was in 6 m on the southern and in 9 m of water on the northern sandflat. In addition, the bed was more than 30 m wider along the northern transect. Therefore, the greater width and seaward depth limits of the sand dollar bed were also associated with stronger wave swell.

CANYON RIDGE TRANSECT

Faunal changes along the canyon ridge transect provide further evidence for the relationship between benthic community zonation and substrate motions. The ridge stations (A through D) traversed a substrate movement or disturbance gradient at a constant water depth of 14 m. Therefore, a number of other environmental factors that changed with water depth along the sandflats did not vary along the ridge transect. These included light, temperature, resuspension and settlement of food particles, and the zonation of predatory demersal fish (see Discussion). On the other hand, there was a distinct gradient of substrate movement along the sandflats as well as along the canyon ridge. The type of sediment movement, however, was rather different. The primary substrate movements along the sandflats were caused by wave-generated, oscillating bottom currents, which became greater with decreasing water depth. Water depth was constant along the ridge. This substrate disturbance gradient was caused by a unidirectional (down-canyon) creeping of sediment which was greater at stations located nearer to the terrace walls and channels (i.e., stations D and C) (see Environmental Setting).

Despite these differences, benthic community zonation was similar along the sandflat and canyon ridge transects. The similarity is partially illustrated by the abundance of polychaetes and crustaceans (Figure 11). The most striking parallels, however, were in the distributions of individual species (Oliver 1979). Species that were highly characteristic of the shallowest sandflat stations (e.g., *Scoloplos armiger, Dispio uncinata, Onuphus eremita, Olivella pycna, Euphilomedes longiseta*) were found at stations D and C along the ridge (zone of sediment slumping). Species that were most abundant at intermediate sandflat depths were found at intermediate ridge stations, C and B (e.g., juvenile *Dendraster excentricus,*

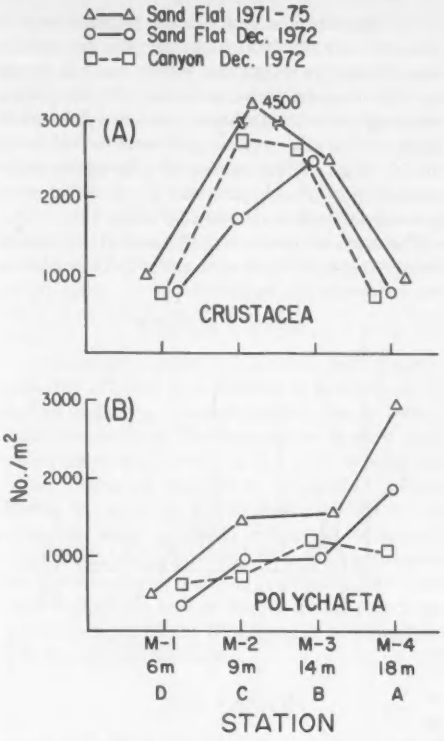

FIGURE 11.—Variations in abundance of crustaceans and polychaetes along the canyon ridge (A-D) and sandflat transects (M) in December 1972, and along the sandflat from 1971 to 1975 in Monterey Bay, Calif.

Eohaustorius sencillus, Euphilomedes carcharodonta). Finally, several polychaetes (*Nothria elegans, Amaeana occidentalis, Lumbrineris luti, Magelona* spp.) that were common in deeper water were most abundant at ridge stations B and especially A (farthest from sediment slumping).

There were only a few statistically significant correlations between the abundance of individual species along the sandflat and canyon transects ($P<0.05$). Since the correlations involved four pairs of stations, there were just 2 degrees of freedom in determining the significance of a product-moment correlation coefficient (Snedecor and Cochran 1967). With 2 degrees of freedom, a significant ($P<0.05$) coefficient must be at least $r = 0.95$. However, there were more positive correlation coefficients computed for the individual species than expected by chance alone. Eighteen of the most abundant 23 species (those inhabiting both transects at >1/core) had positive coefficients. Assuming no correlation between the two transects (i.e., independence), the probability of 18 positive correlation coefficients is 0.019 (sign test, Snedecor and Cochran 1967). The probability is less when only the species with relatively distinct zonation patterns are considered ($P<0.01$). The average correlation coefficient among these species is 0.54 ± 0.12 (95% CL). Therefore, although few individual species showed a statistically significant correlation in abundance along the sandflat and canyon transects, there was a significant trend in positive correlation when the abundant species were considered together.

In summary, benthic community zonation along the gently sloping sandflats (6-18 m) was similar to the zonation along a constant depth transect on the canyon ridge (14 m). This similarity was observed despite differences in substrate disturbance (oscillating vs. unidirectional creeping) and transect lengths (almost 1 km vs. 40 m).

SEASONAL PATTERNS

Seasonal changes in polychaete abundance were more regular than those of the crustaceans (Figures 12, 13). The lowest polychaete abundance generally occurred in the late fall and the winter (Figure 12). The most dramatic population de-

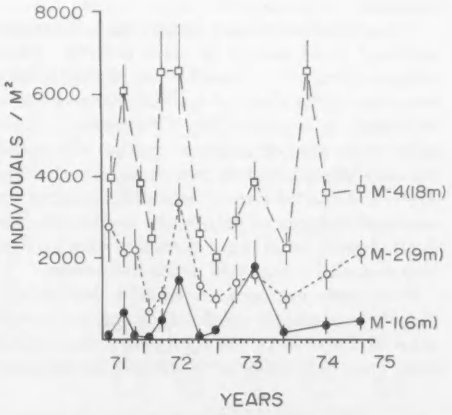

FIGURE 12.—Temporal variations in number of polychaete individuals at three depths along the southern sandflat in Monterey Bay, Calif. (means and 95% confidence limits).

FIGURE 13.—Temporal variations in number of crustacean individuals along the southern transect in Monterey Bay, Calif. (means and 95% confidence limits).

creases, to zero in some cases, were at the shallowest station (Figure 12; M-1, 6 m). Because of the shallow water depth, wave-induced substrate motions were most severe at this station (see Environmental Setting). Furthermore, seasonal substrate movements were greatest during the late fall and winter, when wave heights were large and wave periods short (Figure 3). Therefore, the lowest polychaete numbers were found during that time (late fall and winter) and at the water depth (6 m) corresponding to the greatest substrate motions.

Many environmental factors had a general seasonal trend similar to wave activity. Water temperature, river runoff, and phytoplankton standing stocks also had marked winter-summer variations in Monterey Bay (Oliver et al.[4]). However, wave-induced sediment motion was one of the only seasonal factors that changed with water depth and was, thus, coincident with the depth and seasonal changes in polychaete abundance. The depth-dependent changes in resuspended particulate material are treated in the discussion.

Prionospio pygmaea, *Armandia brevis*, and *Magelona sacculata* settled into the crustacean zone (M-1 and M-2), but rarely survived to adult size. Their frequency of occurrence at the shallower stations was much lower than it was in deeper water (Table 2). Moreover, the low population abundance during the winter was not simply a result of seasonal changes in larval availability. Although some polychaete species appeared to have a relatively seasonal pattern of larval availability (e.g., *M. sacculata*), the larvae of other species (e.g., *N. elegans* and *P. cirrifera*) were present throughout the year (Figure 14).

The seasonal peaks in polychaete abundance in deeper water (M-4, 18 m) were largely due to the

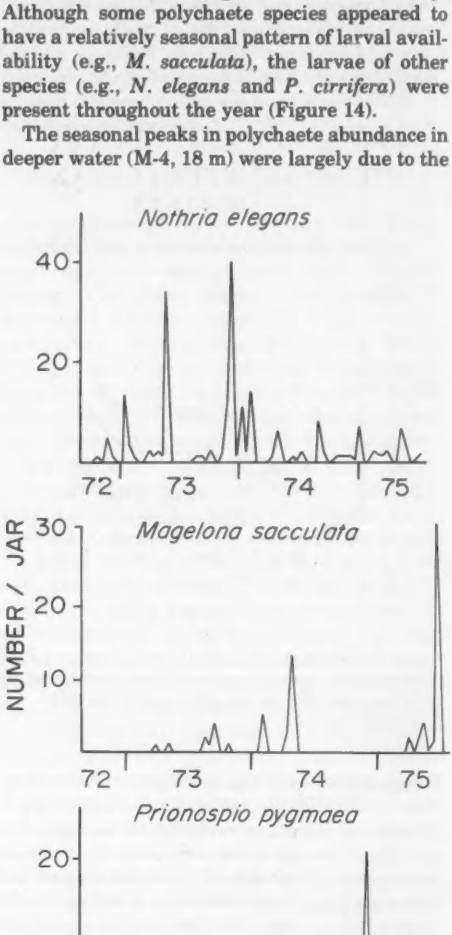

FIGURE 14.—Abundant sandflat polychaetes collected in larval settling jars at the 18 m station (M-4) in Monterey Bay, Calif.

[4]Oliver, J. S., P. N. Slattery, L. W. Hulberg, and J. W. Nybakken. 1977. Patterns of benthic succession after dredging and dredge material disposal in Monterey Bay, California. U.S. Army Corps Eng. Waterways Exp. Stn., Tech. Rep. 0-77-27, 186 p.

settlement of *M. sacculata*. The correlation of the abundance of *M. sacculata* with the total number of polychaetes at M-4 was highly significant ($r = 0.71$; $P<0.001$). *Magelona sacculata* generally accounted for about one-quarter of the polychaete numbers at M-4. As a result, polychaete abundance patterns in deeper water were dominated by seasonal changes in larval availability (Figure 14) and recruitment, and were not clearly related to substrate motions. This correlation between the abundance of *M. sacculata* and the total polychaete numbers decreased in shallower water (M-2, 9 m: $r = 0.34$, $P>0.1$; M-1, 6 m: $r = 0.39$, $P>0.1$).

In summary, seasonal abundance patterns were probably affected by a number of environmental factors including seasonal reproductive cycles and substrate motions. The recruitment or survival of polychaetes was lowest at the time of year and water depth of maximum substrate motions. Hence, the zonation of polychaetes in the crustacean zone was apparently influenced by seasonal changes in wave-induced substrate movements. On the other hand, seasonal variations in crustacean abundance and in deeper living polychaete populations could not be related to sediment motion in a simple manner.

DISCUSSION

The general zonation of benthic invertebrate communities observed in central Monterey Bay is common along much of the temperate open coast of western North America. Carey (1965, 1972), Lie (1969), and Lie and Kisker (1970) observed a high abundance of crustaceans at their shallowest sampling stations and the numerical dominance of polychaetes in deeper areas off Oregon and Washington. Barnard (1963) and VanBlaricom (1978) found the same two zones in southern California and Hodgson and Nybakken (1973) described a comparable pattern in the northern part of Monterey Bay. A similar change from a crustacean- to a polychaete-dominated assemblage was also related to wave exposure by Masse (1972) in the Mediterranean. On the other hand, Day et al. (1971) and Field (1971) did not find a rich crustacean fauna in the "turbulent" zone they described in 3-20 m on the continental shelves of North Carolina and False Bay, South Africa, respectively.

The composition of the fauna along the sandflats was similar to that found at comparable depths in southern California, but the animal density in Monterey Bay was almost a power of 10 greater (compare Table 2 with Barnard 1963). This disparity was greatest in the crustacean zone. The differences are probably related to different sampling methods: diver corers contrasted to the orange-peel grab used in the earlier studies.

None of the previous studies provide convincing evidence for a relationship between community zonation and wave-induced substrate motions. Although the evidence from the present study is descriptive and correlative, it is consistent with many observations. The general hypothesis is that wave-induced sediment movement has a strong influence on community zonation along the subtidal high-energy beach.

Some of the strongest evidence supporting this hypothesis comes from the natural history patterns of the fauna. There was a significant positive correlation ($r = 0.92$, $P<0.05$) between the water depth of a station and the numbers of tube builders, burrow dwellers, and commensal animals. A similar trend emerges when the animals are grouped into mobile and sedentary forms (Figure 15). Apparently, biogenic structures were difficult or impossible to establish and maintain in areas of more intense physical sediment movement. Although wave disturbance might destroy burrows and tubes and dislodge their inhabitants, some adults were tolerant of heavy sediment accumulations and capable of vertical substrate migrations (e.g., *Nothria elegans*). The zonation of polychaetes may be largely determined by the habitat selection of settling larvae (Oliver 1979).

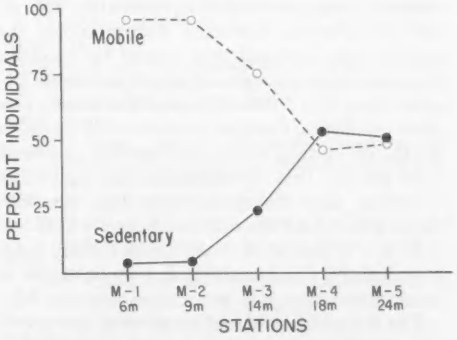

FIGURE 15.—Variations in animal motility patterns along southern sandflat in Monterey Bay, Calif. (percentage of total individuals).

Other natural history patterns also support the relationship between community zonation and substrate motion. In particular, the small peracarid and ostracod crustaceans seem well suited for life in the shifting substrate of the crustacean zone. Their durable chitonous exoskeleton and general activity probably ensure a greater survival relative to many soft-bodied and more sessile forms. Furthermore, their brooding habit and the parturition of large, armoured juveniles undoubtedly increased recruitment success. While no general pattern of crustacean mobility characterized a particular depth, almost all the crustaceans were active burrowers and few maintained a permanent tube or burrow. The lack of dependence on such structures is probably important to the persistence of these large, shallow-water populations. In addition, the most frequently occurring polychaetes in the crustacean zone were also active burrowers that did not live in permanent tubes or burrows.

Variations in zonal patterns along the two sandflats also support the wave-disturbance hypothesis. Wave activity and therefore bottom disturbance were greater along the northern sandflat, where faunal zones were wider and shifted into deeper water. At least one seasonal change in zonation was coincident with an increase in wave activity. The season (late fall and winter) and location (shallowest station, M-1, 6 m) of the greatest wave-induced bottom currents were characterized by the lowest recruitment and survival of polychaetes.

The last source of evidence supporting the hypothesis involves the canyon. While the gradient of substrate motion along the sandflat was caused by waves intercepting a shoaling bottom, the gradient of substrate motion along the canyon ridge transect was caused by unidirectional sediment slumping at a constant depth. Despite these very different types of sediment movement gradients, changes in community zonation along the canyon ridge and sandflat transects were similar. This result negates the importance of several other ecological factors that vary with water depth along the sandflat, but were held constant by the canyon contrast. These include light, temperature, the deposition and resuspension of fine food particles, and the zonation of bottom fish.

The deposition and resuspension of fine particles, which might be used as food, depend upon bottom currents. The strongest bottom currents were caused by wave swell (see Environmental Setting). These oscillatory bottom currents are highly dependent upon water depth and other factors that did not vary along the canyon ridge transect. Thus, while there were probably significant variations in the availability of suspended particles to the different sandflat stations (i.e., their fauna), deposition and resuspension were apparently uniform along the canyon transect.

Demersal flatfish have a zonation that coincides with the zonation of bottom invertebrates. Many species of fish become more abundant with increasing water depth and are more common in the polychaete zone (Table 5). The only species that was numerous in <20 m was the speckled sanddab, *Citharichthys stigmaeus*. Its peak abundance, however, was in 14-18 m and decreased markedly in shallower depths (Ford 1965; Kukowski 1973). Since these flatfish are major predators of sand-bottom invertebrates and they primarily feed by sight (Ford 1965; VanBlaricom 1978; Hulberg and Oliver 1979), active, surface-dwelling crustaceans might be particularly susceptible prey. If this is true, the depth-related increase in bottom feeding fish might account for the correlated decrease in the shallow-water crustaceans. The changes in community zonation along the canyon ridge do not support this idea. Large and highly mobile flatfish can easily patrol the entire length of a 40 m transect.

In summary, trends in the natural history of the animals, changes in zonal patterns along the southern and northern sandflats, seasonal patterns of polychaete recruitment and survival in the shallows, and the similarity between the canyon and sandflat transects support the contention that community zonation is influenced by changes in wave-induced bottom disturbance. Alternate explanations concerning changes in physical sedimentary parameters (Table 1), the availability of suspended food, and the zonation of large flatfish are not consistent with as many observations. One potentially important alternate hypothesis could not be evaluated here. This is the effect of active crustaceans on the settlement and

TABLE 5.—Total number of species and individuals of fish and abundance of the three most common demersal flatfish in otter trawls taken in Monterey Bay, Calif. (from Kukowski 1973).

Item	15 m	36 m
No. species[1]	7.7	13.8
No. individuals	239	359
Citharichthys stigmaeus	33	12
C. sordidus	14	120
Parophrys vetulus	10	33

[1]Mean number caught per 10-min tow with 20 tows at each depth.

early survival of polychaete larvae in the crustacean zone.

The most disruptive wave disturbances were caused by the mass accretion and erosion of the substrate by heavy storm swells. The local sedimentary structures indicated that severe scouring occurred at a water depth of at least 10 m and numerous diving observations revealed significant sediment movement at the deepest study stations. These periodic and catastrophic disturbances are probably more important in maintaining the zonal patterns than the average wave activity of the region. In either case, wave-induced substrate motion undoubtedly prevents the establishment and restricts the activities of many animals and directly or indirectly controls community zonation.

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DAILY TIME OF SPAWNING OF 12 FISHES IN THE PECONIC BAYS, NEW YORK

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ABSTRACT

Diel spawning periodicity occurs throughout the spawning season in 11 of 12 fishes studied in the Peconic Bays, New York. The bay anchovy, *Anchoa mitchilli*; Atlantic menhaden, *Brevoortia tyrannus*; northern and striped searobins, *Prionotus carolinus* and *P. evolans*; hogchoker, *Trinectes maculatus*; weakfish, *Cynoscion regalis*; windowpane flounder, *Scophthalmus aquosus*; and butterfish, *Peprilus triacanthus*, spawn primarily in the evening or at night. The tautog, *Tautoga onitis*, and cunner, *Tautogolabrus adspersus*, begin spawning in the afternoon and spawning continues into the night. Scup, *Stenotomus chrysops*, spawns in the morning, and Atlantic mackerel, *Scomber scombrus*, spawns throughout the day.

The prevalence of nocturnal spawners in the Peconic Bays is inconsistent with predictions of hypotheses attributing diel spawning periodicity to reproductive isolation and visual constraints. Some possible causes of diel spawning periodicity are reproductive synchronism between the sexes, deleterious effects of sunlight on embryogenesis, and parent or embryo predator avoidance.

In his review, Woodhead (1966) cited several references indicating that spawning occurs only in the evening or at night in some clupeids, gadids, pleuronectids, exocoetids, and mullets, and only during daylight hours in some gobies, blennies, and pomacentrids. Woodhead concluded: "There is relatively little direct information describing the spawning behaviour of marine fish, but such as is available suggests that spawning is restricted to a particular part of the day." Recent research generally supports that conclusion.

Simpson (1971) determined the time of day of spawning of four marine fishes from the occurrence of recently spawned eggs in plankton collections. His results showed spawning occurs in plaice, *Pleuronectes platessa*, between 1800 and 0700 h; sprat, *Sprattus sprattus*, between 2200 and 0600 h; pilchard, *Sardina pilchardus*, between 2000 and 0200 h; and throughout the day in dab, *Limanda limanda*, but most intensely between 2400 and 1200 h. Wicklund (1970) observed that natural spawning of small (total length <125 mm) cunner, *Tautogolabrus adspersus*, was restricted to between 1200 and 1700 h. A sevenfold difference in numbers of fish eggs in night vs. day plankton collections prompted Hobson and Chess (1978) to suggest that many reef fishes primarily spawn at night. Ten anchovy species in the Gulf of Panama have daily spawning periods lasting about 3 h, and all spawn between about 1700 and 0430 h (Simpson 1959).

Accumulating evidence indicates that diel spawning periodicity is a common phenomenon in marine fishes. In this paper further information is presented on daily spawning times of 12 marine fishes from 10 families.

METHODS

From midspring to late fall 1972, 1973, and 1974 plankton collections were taken usually at 9-13 locations in the Peconic Bay area, Long Island, N.Y. (Figure 1). In 1972 and 1973 samples were taken on two consecutive days at intervals of 5-11 days. In 1974 samples were collected at monthly intervals. All collections were made during daylight hours from 0600 to 1735 h e.s.t. At least three vertical plankton-haul samples were taken from the bottom (or to a maximum depth of 12 m) to the surface at each location with a No. 3 (0.333 mm mesh) conical plankton net with a mouth area of 0.5 m^2. The plankton samples were killed and preserved in 4% seawater Formalin[2] and stored in 1 l glass jars. Surface water temperature and solar time of day (hours since sunrise; time of sunrise

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[2]Reference to trade names does not imply endorsement by the State University of New York at Stony Brook, Stony Brook, N.Y., or the National Marine Fisheries Service, NOAA.

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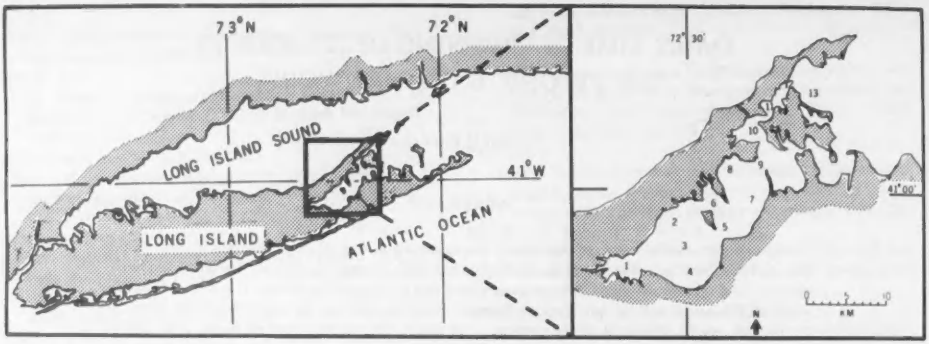

FIGURE 1.—Location of study site and 13 sampling stations in the Peconic Bays, Long Island, N.Y.

from National Ocean Survey 1971, 1972, 1973) of each collection were recorded. Since Peconic Bay waters are well mixed (Hardy 1976), the surface water temperatures were adequate indicators of temperatures of the water column and the natural incubation temperatures of recently spawned fish eggs (see Discussion section).

Over the 3-yr period more than 2,600 samples were collected and processed. Plankton samples were split into manageable subsamples and their entire contents were viewed under a stereomicroscope. Fish eggs were separated, identified to species, staged (Table 1), and counted. Developmental stages in Table 1 are approximately equal in duration when fish embryos are reared at constant temperatures (Ferraro 1980). References used for fish egg identification included: Kuntz (1915), Kuntz and Radcliffe (1917), Hildebrand and Cable (1930, 1934), Merriman and Sclar (1952), Wheatland (1956), Richards (1959), Mansueti and Hardy (1967), Williams (1967), Austin (1973), Berrien (1975), and Colton and Marak[3].

Estimates of time of day of spawning for each species in a sample were determined by estimating the mean age of fish eggs <24 h old using embryo age prediction equations for Atlantic menhaden, *Brevoortia tyrannus*, in Ferraro (1980), below:

$$\log_{10} B = -0.193 + 17.193\,T^{-1} + 34.090\,T^{-2} - 461.276\,T^{-3} \quad (1)$$

[3]Colton, J. B., Jr., and R. R. Marak. 1969. Guide to identifying the common planktonic fish eggs and larvae of Continental Shelf waters, Cape Sable to Block Island. Bur. Commer. Fish. Lab., Woods Hole, Mass., Lab. Ref. No. 69-9, 43 p.

TABLE 1.—Fish embryo stages of development.

Stage	Description
1	Fertilized eggs prior to cell division to 8-cell stage
2	Eight-cell stage to completion of blastodisc formation
3	Blastodisc formation to germ ring ½ way around egg
4	Germ ring ½ way around egg to just prior to blastopore closure
5	Blastopore closure to tail bud beginning to separate from the yolk
6	Tail bud free of yolk to caudal ⅛ of body free of the yolk
7	Caudal ⅛ of body free of yolk to caudal ¼th of body free of yolk
8	Caudal ¼th of body free of yolk to fin fold moderately wide and tail portion of embryo rotated out of embryonic axis and tail approaching head
9	Tip of tail approaching head to hatching

and,

$$A = B\,(S - 1) \quad (2)$$

where B = development time (hours) per stage of development
T = temperature (in degrees Celsius)
S = stage of development (Table 1)
A = mean age (in hours)

and subtracting these values from the time the samples were collected in the field. (Field data on differences in development stages of embryos from consecutive day classes indicated that the *B. tyrannus* embryo age equations introduced little or no error when estimating embryo ages of <24 h of most of the species in this study (see Results).)

RESULTS

Discrete day classes of fish eggs of most species were identified in the field samples. Fish eggs were present in samples at distinct morphological stages of development while other morphological

stages were completely absent. Spring spawners typically had polymodal embryonic stage frequency distributions with one or more embryonic stages absent between adjacent modes. As water in the Peconic Bays warmed, the number of modes in the embryo stage frequency distribution decreased such that by midsummer the distribution was unimodal. Also, as water temperature increased the most recently spawned eggs of most fishes were found at consistently later stages of development.

Indirect evidence from field data indicated that embryonic development rates of most species in this study were similar. Tests of differences between modes of embryo development stages representing two consecutive day classes from field samples at 17° C by a posteriori sums of squares simultaneous testing procedure (Sokal and Rohlf 1969) indicated no significant difference ($P>0.05$) in embryonic growth per day of *B. tyrannus*; bay anchovy, *Anchoa mitchilli*; tautog, *Tautoga onitis*; *Tautogolabrus adspersus*; and searobins, *Prionotus* spp. Also, age differences between day classes of fish embryos in field samples at temperatures between 15.0° and 17.5° C were calculated using the *B. tyrannus* embryo age prediction Equations (1) and (2). The results (Table 2) showed that the *B. tyrannus* equations gave good predictions of the expected age difference between embryo day classes for most of the species in this study.

With the exceptions of scup, *Stenotomus chrysops*; Atlantic mackerel, *Scomber scombrus*; and to a lesser extent *Tautoga onitis* and *Tautogolabrus adspersus* very few early-cleavage stage eggs were collected in our daytime sampling program.

TABLE 2.—Mean age differences ($\bar{x}$, in hours) of fish embryos representing two consecutive day classes in field samples at temperatures[1] between 15.0° and 17.5° C determined by development stage differences between day classes and embryo age prediction equations for *Brevoortia tyrannus*. The expected age difference is 24 h.

Species	Number of samples	$\bar{x}$±SE
Brevoortia tyrannus	124	25.6±0.40
Anchoa mitchilli	53	21.8±0.31
Stenotomus chrysops	20	20.5±0.48
Cynoscion regalis	15	25.4±1.21
Tautoga onitis	101	24.9±0.43
Tautogolabrus adspersus	53	23.6±0.77
Peprilus triacanthus	4	24.2±1.57
Prionotus spp.	64	22.0±0.39
Scophthalmus aquosus	7	22.0±3.16

[1]Range of temperatures chosen were temperatures at which at least two fish embryo day classes would be present.

Mean daily spawning times of fishes were calculated from hourly time of spawning frequency distributions of sample estimates of spawning time (Table 3). The 1974 data were used to compute estimated spawning times of *Stenotomus chrysops*; weakfish, *Cynoscion regalis*; windowpane flounder, *Scophthalmus aquosus*; and butterfish, *Peprilus triacanthus*, and only 1973 data were used to compute the spawning time of the hogchoker, *Trinectes maculatus*. Time of spawning estimates were similar for species where data were available for 2 yr. Histograms of relative frequency distributions of sample estimates of spawning time are presented for 1973 data on *Anchoa mitchilli*; *Brevoortia tyrannus*; *Tautoga onitis*; *Tautogolabrus adspersus*; northern and striped searobins, *Prionotus carolinus* and *P. evolans* (note: the searobins are considered together because their embryos can not be reliably distinguished); and *Trinectes maculatus* in Figure 2. In summary, the results show that *A. mitchilli*, *B. tyrannus*, *P. carolinus*, *P. evolans*, *T. maculatus*, *C. regalis*, *S. aquosus*, and *Peprilus triacanthus* spawn primarily in the evening or at night; *Tautoga onitis* and *Tautogolabrus adspersus* spawn in the afternoon and at night; and *Stenotomus chrysops* spawns in the morning.

There was no evidence of diel spawning periodicity by Atlantic mackerel. Typically, all developmental stages (Table 1) were present in samples containing Atlantic mackerel eggs. The only general trend in the Atlantic mackerel egg data was a decrease in numbers of later developmental stages, presumably due to dispersion or egg mortality.

TABLE 3.—Mean daily spawning times ($\overline{DST}$, in hours after sunrise) of fishes calculated from hourly frequency distributions of sample estimates of spawning time. Estimated ages of fish eggs <24 h old in field samples were subtracted from their time of collection to obtain sample estimates of spawning time.

Species	Year	*N*	$\overline{DST}$±SE
Brevoortia tyrannus	1972	198	16.36±0.175
	1973	370	17.84±0.168
Anchoa mitchilli	1972	455	16.09±0.103
	1973	693	16.78±0.078
Stenotomus chrysops	1974	32	5.28±0.276
Cynoscion regalis	1974	74	17.45±0.407
Tautoga onitis	1972	160	15.52±0.200
	1973	447	17.62±0.126
Tautogolabrus adspersus	1972	101	15.40±0.343
	1973	322	15.98±0.215
Peprilus triacanthus	1974	22	18.55±0.881
Prionotus spp.	1972	174	19.19±0.307
	1973	330	19.15±0.197
Scophthalmus aquosus	1974	38	16.68±0.607
Trinectes maculatus	1973	132	16.55±0.110

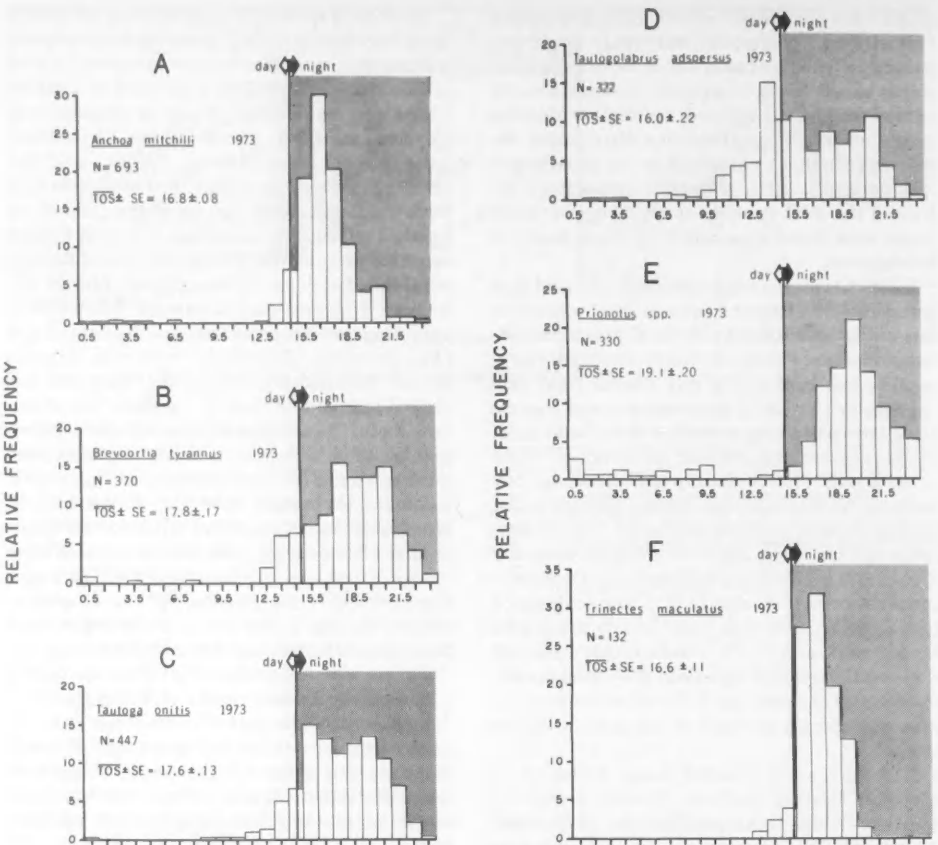

FIGURE 2.—Relative frequency distributions of estimated spawning times (TOS) of (A) *Anchoa mitchilli*, (B) *Brevoortia tyrannus*, (C) *Tautoga onitis*, (D) *Tautogolabrus adspersus*, (E) *Prionotus* spp., and (F) *Trinectes maculatus*, determined by subtracting estimated mean ages of fish eggs <24 h old from their time of collection in 1973 samples. Mean day length during spawning seasons is indicated.

DISCUSSION

Direct observation of fish spawning at sea is rare, and aquarium observations may not be characteristic of natural spawning or may be difficult or impractical to implement for logistic reasons. Since embryogenesis begins at spawning in most marine teleosts, the time of day spawning occurs can be determined indirectly from the age of embryos captured at sea. Several investigators, including Ahlstrom (1943), Gamulin and Hure (1956), and Simpson (1971), collected plankton samples throughout the day and determined spawning times of fishes from the occurrence of recently spawned eggs. Under certain circumstances (when field temperatures are fairly constant and there is little translocation of eggs) and with knowledge of embryonic development rates, however, spawning times can be back calculated by subtracting age of fish embryos from their time of collection. The method of estimating spawning time of fishes in this paper utilizes field

data commonly obtained in ichthyoplankton research and does not require a continuous field sampling program.

Factors influencing the accuracy of estimated spawning times of fishes in this paper are intraspecific and interspecific differences in development rates of fish embryos and temperature effects on embryo stage (Table 1) duration. Intraspecific differences in development rates are likely to introduce only small and unbiased error in spawning time estimates since incubation times from which age estimates are made are short (<24 h) and mean stages of development of all embryos of a species (<24 h old) in a sample are used in the embryo age calculation. Interspecific differences in development rates of most species in this study are also probably small (see Results). A maximum standard deviation of 2.3 h can be expected in spawning time estimates due to the influence of temperature on embryo stage duration because most fish eggs were collected in water temperatures above 15° C (Ferraro 1980). Surface water temperatures at the time of field collection were probably adequate indicators of natural incubation temperatures of recently spawned eggs since there is little, if any, vertical thermal stratification in the Peconic Bays and surface water temperature at a particular location generally fluctuates by <1° C during a tidal cycle (Hardy 1976).

Based on the occurrence of recently spawned eggs in plankton collections at Beaufort, N.C., Kuntz (1915) and Hildebrand and Cable (1930) concluded that *A. mitchilli* spawned between 1800 and 2100 h (13-16 h after sunrise), and Hildebrand and Cable (1938) concluded that *Trinectes maculatus* spawned between 1800 and 2000 h (13.5-15.5 h after sunrise). Those observations coincide with the onset of spawning estimated for *A. mitchilli* and *T. maculatus* in this paper. Reintjes' (1968) conclusion that *B. tyrannus* spawns at night, Welsh and Breder's (1924) conclusion that *C. regalis* spawns in the evening and at night, and Sette's (1943) calculations showing *Scomber scombrus* spawns throughout the day were confirmed in this research. Wicklund's (1970) observations on the spawning of cunner overlap but have a much shorter duration than that indicated for cunner in Figure 2D. Wicklund (1970) only observed spawning by small (total length <125 mm) cunners between 1200 and 1700 h (7-12 h after sunrise); he never observed larger cunners spawning although they were present and defended territories in his study area. Olla and Samet (1977) noted that tautog in laboratory aquaria spawned almost exclusively between 1330 and 1600 h (7.5-10 h after sunrise). Their experimental fish, however, had been exposed to unnatural photoperiod and temperatures and spawned about 2 mo earlier than tautog normally spawn in nature. Recently spawned eggs in plankton collections indicated that some tautog spawn in the afternoon (8-10 h after sunrise) in the Peconic Bays, but the bulk of tautog spawning appears to take place later in the evening and at night.

A systematic division of fishes in the Peconic Bays and a summary of their spawning times is presented in Table 4. Only Atlantic mackerel showed no indication of diel spawning periodicity, and only scup spawned exclusively during daylight hours. The remaining species spawned primarily during the evening or at night. Nothing exceptional is known about the adult habits or embryos of Atlantic mackerel or scup to suggest why their spawning times are different from the other species. There appears to be no connection between bathymetric distributions of embryos of some of the species (Williams 1968) and spawning time. There was no evidence of constancy in spawning time above the family level. Solar spawning times of most species, though, were consistent throughout the spawning season and in samples collected at different locations, indicating seasonal and local differences in ecologic factors (e.g., temperature, salinity, water depth, tide) had no effect on daily spawning time.

The tendency of marine teleosts with planktonic eggs to spawn in the evening or at night is evident in a listing (Table 5) of some species known or suspected of diel spawning periodicity. There is

TABLE 4.—Systematic division and summary of spawning times (hours after sunrise) of fishes in the Peconic Bays, N.Y. Spawning is indicated by +.

Taxa	Species	Spawning time 0-6	6-12	12-18	18-24
Clupeiformes:					
Clupeidae	*Brevoortia tyrannus*			+	+
Engraulidae	*Anchoa mitchilli*			+	+
Perciformes:					
Sparidae	*Stenotomus chrysops*	+			
Sciaenidae	*Cynoscion regalis*			+	+
Labridae	*Tautoga onitis*		+	+	+
	Tautogolabrus adspersus		+	+	+
Scombridae	*Scomber scombrus*	+	+	+	+
Stromateidae	*Peprilus triacanthus*			+	+
Triglidae	*Prionotus carolinus*			+	+
	Prionotus evolans			+	+
Pleuronectiformes:					
Bothidae	*Scophthalmus aquosus*			+	+
Soleidae	*Trinectes maculatus*			+	

TABLE 5.—Some marine teleosts which spawn planktonic eggs and are known or suspected of spawning only at particular times of the day.

Family and species	Spawning time	Reference
Ophichthidae:		
Pisodonophis cruentifer	Night	Naplin and Obenchain (1980)
Clupeidae:		
Etrumeus teres	Night	Houde (1977)
Sardinella melanosticta	Night	Kamiya (1925)
Sardinops sagax	Evening	Ahlstrom (1943)
Sardinia pilchardus	Evening and night	Gamulin and Hure (1956); Simpson (1971)
Sprattus sprattus	Night	Simpson (1971)
Engraulidae:		
Anchoa hepsetus	Evening and night	Hildebrand and Cable (1930)
A. mitchilli	Evening and night	Kuntz (1915); Hildebrand and Cable (1930)
Cetengraulis mysticetus	Night	Simpson (1959)
Engraulis eurystole	Evening	Kuntz and Radcliffe (1917)
E. mordax	Night	Bolin (1936)
Engraulis spp.	Evening	Delsman (1929)
Stolephorus purpureus	Night	Yamashita (1951)
Stolephorus spp.	Night	Delsman (1931)
Antennariidae:		
Histrio histrio	Afternoon and evening	Walters (pers. commun. in Breder and Rosen 1966)
Gadidae:		
Enchelyopus cimbrius	Morning	Battle (1930)
Gadus morhua	Evening and night	Brawn (1961); Breder and Rosen (1966)
Merluccius merluccius	Morning	Storrow (1913)
Pomatomidae:		
Pomatomus saltatrix	Evening	Norcross et al. (1974)
Carangidae:		
Caranx kurra	Night	Delsman (1926)
C. macrosoma	Night	Delsman (1926)
C. crumenophthalmus	Night	Delsman (1926)
Pomadasyidae:		
Orthopristis chrysoptera	Evening	Hildebrand and Cable (1930)
Sciaenidae:		
Bairdiella chrysura	Evening	Kuntz (1915)
Cynoscion nebulosus	Night	Tabb (1966)
C. regalis	Evening and night	Welsh and Breder (1924)
Labridae:		
Tautoga onitis	Afternoon	Olla and Samet (1977)
Tautogolabrus adspersus	Afternoon	Wicklund (1970)
Scaridae:		
Scarus croicensis	Afternoon	Colin (1978)
Sparisoma rubripinne	Afternoon	Randall and Randall (1963)
Mugilidae:		
Mugil cephalus	Night	Arnold and Thompson (1958)
M. curema	Night	Anderson (1957)
Scombridae:		
Scomber japonicus	Night	Kamiya (1925)
Scomberomorus maculatus	Evening and night	Ryder (1882); Rathbun (1894); Smith (1907)
Pleuronectidae:		
Hippoglossus hippoglossus	Night	Nordgård (1929)
Pleuronectes platessa	Night	Forster (1953); Simpson (1971)
Pelotretis flavilatus	Night	Thomson and Anderton (1921)
Colistium nudipinnis	Night	Thomson and Anderton (1921)
C. guntheri	Night	Thomson and Anderton (1921)
Peltorhamphus novaezeelandiae	Night	Thomson and Anderton (1921)
Rhombosolea plebeia	Night	Thomson and Anderton (1921)
R. tapirina	Night	Thomson and Anderton (1921)
Soleidae:		
Trinectes maculatus	Evening	Hildebrand and Cable (1938)

diel and lunar spawning periodicity in some coral reef fishes (e.g., Lobel 1978; Johannes 1978; May et al.1979). References cited in Breder and Rosen (1966) indicate that at least 70 freshwater and marine teleosts with demersal or attached eggs may spawn or oviposit at particular times of the day. Even though many of the data are only suggestive, there are indications that diel spawning periodicity may be a common and widespread phenomenon among fishes.

Diel spawning periodicity in fishes may be due to physiological constraints or may be adaptive. Woodhead (1966) and Blaxter (1965, 1970) pointed out that light may restrict spawning to a particular time of day, especially in species where vision is important in sexual displays, courtship, and pairing. Woodhead (1966) noted, however, that species which require daylight for courtship might still spawn or oviposit at other times of the day. Obviously, nocturnal spawners are not light limited. If adaptive, the value of reproductive periodicity may be found in the synchronization of reproduc-

tion with the biotic or abiotic environment (Nikolsky 1963; Aschoff 1964; Schwassman 1969). The annual spawning cycle of fishes which may be timed to coincide with the annual production cycle, or a period of low predation, etc. (Nikolsky 1963; Cushing 1969; Hoar 1969), may be the coarse adjustment, and diel spawning time the fine tuning adjustment to temporally changing environmental conditions.

Spawning periodicity may be important in synchronizing reproduction between the sexes (Aschoff 1964; Marshall 1967). The precise daily timing of reproduction may be particularly important in species which engage in mass spawnings. An extreme example are the lancelets (e.g., *Branchiostoma lanceolatum*) which, according to Breder and Rosen (1966), release eggs and sperm into the water at sunset for chance fertilization. Temporally synchronizing spawning in pairing species presumably is more efficient and may optimize the number of receptive encounters.

Marshall (1967) suggested diel spawning periodicity might serve to increase reproductive isolation between related and morphologically similar species. Reproductive isolation may be important in a species-rich habitat such as a coral reef, but many temperate water marine fishes apparently spawn at or about the same time, i.e., in the evening and at night (Tables 4, 5).

Diel spawning periodicity could be an adaptive behavior of fishes to avoid high incident solar radiation during a very sensitive period of embryonic development. Bell and Hoar (1950) and Eisler (1958, 1961) demonstrated the lethal and deleterious effects of light on salmonid embryos, especially during early embryogenesis; and Marinaro and Bernard (1966) demonstrated lethal effects of light, particularly ultraviolet light, on some marine planktonic fish embryos. Perlmutter (1961) and Breder (1962) believed that some characteristics of fish eggs (e.g., transparency, oil droplets, melanophores) were physiological adaptations to minimize deleterious effects of light on fish embryos, and Perlmutter (1961) listed several spawning behaviors of fishes which he thought were adaptions to avoid or minimize exposure of embryos to light. If light is especially harmful to recently fertilized fish eggs, nocturnal spawning could be an adaptive behavior to avoid light during early embryonic development. However, an explanation is then necessary for why light is not a factor for diurnal spawners such as Atlantic mackerel and scup.

Nikolsky (1963) suggested that some fishes spawn at times of day when spawning adults or their eggs will be least susceptible to predation. The "exhausted" condition of some fishes that have recently spawned (Brawn 1961; Breder and Rosen 1966) and evidence of increased vulnerability of some spawning fishes to trawling (Mohr, in Blaxter 1965) tend to support the idea that spawning time may be an adaption to minimize losses due to predation on the parents. Visual predators, predators with diurnal feeding patterns, or predators which undergo diurnal vertical migrations (e.g., ctenophores; Hirota 1974) could subject planktonic fish embryos to different levels of predation over a diurnal cycle. Synchronizing daily spawning time to coincide with a period of low fish embryo predation minimizes fish embryo mortality due to predation. If a fish embryo predator had a diurnal predation cycle of 12 h high and 12 h low predation, Figure 3 shows that a fish spawning at the beginning of a low predation period ensures 50% or more of the embryo incubation time of its progeny will be spent at the low predation level. Qualitatively the results would be the same if changes in predation were gradual and periods of high and low predation were of different durations. Figure 3 also shows that if predation cycles cause diel spawning periodicity, selection for diel spawning periodicity is potentially greater when embryo incubation times are short.

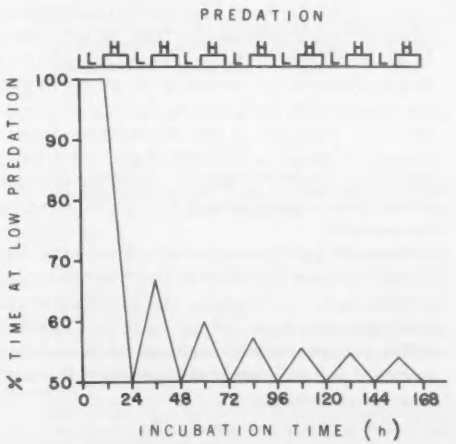

FIGURE 3.—Relationship between percentage of time spent at low predation when spawning occurs at the beginning of a period of low predation and total incubation time of embryos, assuming 12 h alternating periods of low (L) and high (H) predation.

The physiological or adaptive cause(s) of diel spawning periodicity in fishes may become clear as data on its occurrence accumulates or by experiments. Effects of natural maximum solar radiation at the sea surface on different development stages of marine planktonic fish embryos should be studied experimentally. Field studies on fish embryo mortality at different times of day, and studies on feeding patterns of major fish embryo predators and adult fish predators during the spawning season could help elucidate or eliminate some of the factors suspected of causing diel spawning periodicity. If correct, one of the implicit consequences of the diurnal predation cycle hypothesis is that diel spawning periodicity should be more common in fishes with short embryo incubation times (Figure 3), and this prediction should be tested. Additional data on diel spawning periodicity in fishes and studies such as those listed above should ultimately provide important insights into fish physiology, reproductive biology, and ecology.

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AN IMPROVED METHOD TO ANALYZE TRIMETHYLAMINE IN FISH AND THE INTERFERENCE OF AMMONIA AND DIMETHYLAMINE

FERN A. BULLARD AND JEFF COLLINS[1]

ABSTRACT

The trimethylamine content of most marine fish, especially the gadoid species, is internationally accepted as an index of spoilage. However, ammonia, dimethylamine, and other amines also contribute to the trimethylamine value. Variations in the conditions of the three current methods used to analyze for trimethylamine content were studied in detail to determine the best condition to extract trimethylamine and to reduce the extraction of ammonia, dimethylamine, and other amines. Formaldehyde does not inhibit the interference from ammonia but the interference is negligible even in advanced spoilage. Formaldehyde inhibits the interference from dimethylamine to some extent if KOH is used as the base but increases the interference in the K_2CO_3 method. The extraction of di- and trimethylamine are highly dependent upon the base used and the temperature of extraction. A new method of extracting at −15° C using 45% KOH was developed that essentially eliminates interference from ammonia, dimethylamine, and other amines. To directly compare the methods, the trimethylamine content of a sample of spoiled walleye pollock, *Theragra chalcogramma*, flesh was determined by the three currently used methods and the cold method of extraction. All methods gave similar standard deviations but the K_2CO_3 method gave higher values than the KOH methods and the cold method gave the lowest value. Various levels of trimethylamine and dimethylamine simulating different qualities of fish and frozen storage times were added to samples of Pacific cod, *Gadus macrocephalus*, flesh. The cold method consistently extracts more accurate amounts of trimethylamine with less interference from dimethylamine than any of the other extraction methods.

The trimethylamine (TMA) content of most marine fish, especially the gadoid species, is accepted internationally as an index of spoilage. Dyer's 1959 method of analysis for TMA, except for the concentration of formaldehyde (FA), has been adopted by the Association of Official Analytical Chemists (Horwitz 1975). Trimethylamine is produced by the reduction of trimethylamine oxide by microorganisms (Poller and Linneweh 1926). Ammonia, dimethylamine (DMA), and other volatile bases are also formed when fish spoil and to some extent interfere with the measurement of TMA. In advanced spoilage, some of the higher aliphatic amines are formed by decarboxylation of amino acids and may cause interference (Dyer 1945).

A number of investigators studied the TMA method to improve the accuracy and reduce the effects of ammonia, DMA, and other amines. Dyer (1945) adapted the method of determining amines to fish and used 0.02% picric acid in dry toluene instead of chloroform (Richter 1938; Richter et al. 1941). Dyer and Mounsey (1945) used a trichloroacetic acid (TCA) extract of fresh cod instead of the unstable press juice or weighed samples. Hashimoto and Okaichi (1957) claimed that variation of temperature caused serious errors in the determination of TMA, and recommended a 30° C extraction with 25% KOH rather than 50% K_2CO_3 and room temperature. Tozawa et al. (1971) confirmed these findings and showed that 25% KOH reduced the interference caused by DMA and claimed the formation of a compound from FA and DMA which was not extracted in the presence of hydroxide ions. Murray and Gibson (1972) found that 45% KOH extracted more TMA and gave more linear and reproducible results than if extracted with 25% KOH or 50% K_2CO_3.

The three current methods of analysis for TMA employ 25% KOH, 45% KOH, or 50% K_2CO_3 to release TMA for extraction into the toluene layer and result in different absorbancies for the picrate color with DMA and TMA. In general, the use of K_2CO_3 results in a higher extraction of DMA and a lower extraction of TMA than if KOH were used. Ideally, the best method to measure TMA content should result in complete extraction of TMA and zero extraction of ammonia (NH_3), DMA, and other amines so that these components will not contribute to the TMA value. A new method was

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developed from information obtained from a detailed study of how temperature, type and concentration of base, and the presence (or not) of FA affect the extraction and subsequent absorbancies of the picrate color of NH_3, DMA, and TMA.

EXPERIMENTAL

Purification Procedures

Trimethylamine hydrochloride (TMA·HCl) and dimethylamine hydrochloride (DMA·HCl) were crystallized twice from hot 2-propanol and dried under high vacuum overnight. Reagent grade and previously used toluene was purified by shaking and partitioning with concentrated sulfuric acid in a separatory funnel followed by water, sodium hydroxide, and water; filtering through anhydrous sodium sulfate (NA_2SO_4); and distilling at 110° C. Reagent grade Formalin[2] (37% FA) was shaken with magnesium carbonate, filtered, and diluted 1:9 with water. Hexamethylenetetramine (HMTA) from Pfaltz and Bauer was crystallized twice from hot 2-propanol or from hot, dry toluene and dried overnight under high vacuum. N N N′N′-tetramethylmethanediamine (TMMD) from Pfaltz and Bauer was distilled using a column packed with glass helices. The first 25 ml fraction (72°-81° C) was discarded, the next 25 ml fraction (81° C) was used for analysis, and the final 25 ml distillate was discarded. Reagent grade ammonium chloride (NH_4Cl) was crystallized twice from hot water and dried under high vacuum overnight.

Extraction Procedure for Fish Flesh

Procedures cited in the literature for the extraction of fish have used a specific amount of flesh plus water or TCA followed by shaking or blending and filtration. These methods assume a specific moisture content of the flesh, a total volume, and a complete extraction or uniform dispersion of TMA in the extract, e.g., 100 g flesh at 80% moisture plus 300 ml TCA solution would give a 1/95 aliquot for a 4 ml sample. To improve accuracy of the method, we used an exhaustive extraction-filtration procedure and dilution to a volume. Details of the procedure are given in the Recommended Procedures section.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Methods of Analyses for TMA

Unless otherwise indicated, the three commonly used methods of analyses for TMA were modified slightly to fit our equipment and to reflect recent advances in the methods. The methods of Dyer (1945), Tozawa et al. (1971), and Murray and Gibson (1972) were used as follows: a 4 ml sample of a standard solution in 5% TCA or a 5% TCA extract of fish flesh was added to a 25 × 150 mm screw top test tube, followed by the addition of 10 ml toluene, 1 ml of 3.7% FA solution, and left to stand 5 min before the addition of 3 ml of base (25% KOH, 45% KOH, or 50% K_2CO_3). The tube was tightly sealed using a gasket of a double layer of 1 mil polyethylene film under the cap and shaken for 15 min at room temperature on a Burrell wrist action shaker modified by building-up the platform 20.3 cm with Styrofoam. After standing several minutes, about 7 ml of the toluene layer were removed and dried with 0.5 g anhydrous Na_2SO_4. After drying, 5 ml were added to 5 ml of 0.02% picric acid in dry toluene and the absorbance was determined at 415 nm on a Gilford modified Beckman D.U. spectrophotometer. A fourth method will be referred to as the "cold method" of extraction and uses 45% KOH (Murray and Gibson 1972) but the extraction is done at −15° C. The details of this method are given in the section on Recommended Procedures.

Standard Curves

Since four distinctly different methods were used to analyze for TMA content, complete blank determinations and standard curves were made for each method. The equations for the regression lines (standard curves) of absorbance on concentration of TMA (micrograms TMA-N/milliliter) for each of the methods were as follows:

25% KOH, room temperature	$Y = 0.071X - 0.007$	(1)
45% KOH, room temperature	$Y = 0.087X - 0.001$	(2)
50% K_2CO_3, room temperature	$Y = 0.067X - 0.012$	(3)
45% KOH, cold (−15° C)	$Y = 0.082X - 0.007$	(4)

where Y = absorbance and X = micrograms TMA-N/milliliter.

The trimethylamine values in milligrams TMA-N/100 g flesh were calculated from these equations and from the total volume (250 ml) of 5% TCA extract, weight of extracted fish flesh (75 g), 4 ml of sample extract per tube, and a dilution factor

(K), if present (e.g., for the cold method use Equation (4)):

$$\frac{(A + 0.007)(250 \text{ ml})(100)(K)}{(0.082)(75 \text{ g flesh})(1{,}000\ \mu\text{g/mg})} = \text{milligrams TMA-N/100 g flesh.} \quad (5)$$

RESULTS AND DISCUSSION

In the following sections, the influence of the presence of FA (or not), the type and concentration of base used, and temperature of extraction were determined separately on each component in the reaction and extraction mixture; i.e., 1) NH_3 and HMTA, 2) DMA and TMMD, and 3) TMA. The four methods were directly compared for precision by replicate analyses of a composite sample of minced fish flesh. Finally, accuracy (recovery of TMA and the interference of DMA) was determined for the four methods by direct addition of known quantities of TMA and DMA.

Reaction of Ammonia

Sprung (1940) reported that FA reacts with NH_3 to form HMTA. Under vacuum distillation conditions at 30° C, the addition of FA to solutions of NH_4Cl and Na_2CO_3 rendered the NH_3 nonvolatile but in the absence of FA, NH_3 was volatile (Benoit and Norris 1942). Dyer (1945) claimed that the addition of 1 or 2 ml of 4% FA did not affect the recovery of TMA, and was sufficient to eliminate the interference of NH_3 up to 10-20 times over the usual concentration of trimethylamine nitrogen. Dyer, however, did not directly study the influence of FA on the development of the picric acid color in the presence of NH_3. Researchers studying the TMA method have followed the prior procedures and used FA to tie up NH_3 in the TMA test.

Standard solutions of NH_4Cl in 5% TCA were prepared and used in the three TMA methods. To simulate various stages of spoilage the concentration ranged from 6.6 to 66 μg N/ml; i.e., 2.2-22.0 mg N/100 g flesh. The absorbancies from the NH_4Cl solutions with and without FA (Table 1, columns 1-6) were low and of questionable significance except if 45% KOH was used. The absorbancies seemed to increase with concentration of NH_4Cl and were about the same whether FA were present or not if 50% K_2CO_3 and 25% KOH were used. Even at the higher concentrations, the absorbancies were low and would contribute little to the TMA value. When 45% KOH was used, the absorbancies were much higher than the absorbancies with the other bases and were not affected by FA except at the higher concentrations. Accordingly, FA and NH_3 did not react under these conditions and NH_3 could contribute to the TMA value. To determine if FA would react with NH_3 at elevated temperatures, the same standard solutions in 5% TCA were treated as before but were preheated in the presence of FA at 60° C for 30 min, cooled to room temperature, and 45% KOH added and extracted in the usual way. The absorbancies of the preheated samples were reduced significantly—see columns 5 and 7 in Table 1. The low absorbancies indicated that FA reacted with NH_4Cl when heated and there was no interference through 26.4 μg N/ml sample. The color development in the samples containing 33.0 μg N/ml and more could be caused by: 1) residual NH_3 through an incomplete reaction with FA, 2) NH_3 through a reverse reaction of the product which is assumed to be HMTA, by the law of mass action or chemical equilibrium, and 3) a partial extraction of HMTA by toluene and subsequent reaction with picric acid.

TABLE 1.—Ammonium chloride or hexamethylenetetramine (HMTA): the absorbancies of picrates in the trimethylamine test as affected by the addition of standard solutions of ammonium chloride or hexamethylenetetramine. Samples (columns 1-10) were extracted at room temperature for 15 min (except 9 and 10 which were extracted at −15° C for 60 s by hand), with formaldehyde (+) and without formaldehyde (0).

NH_4Cl or HMTA (μg N/ml)	NH_4Cl 50% K_2CO_3		NH_4Cl 25% KOH		NH_4Cl 45% KOH		NH_4Cl/HMTA 45% KOH		NH_4Cl 45% KOH	
	1 +	2 0	3 +	4 0	5 +	6 0	7[1] +	8 0	9 +	10 0
6.6	0.008	0.000	0.001	0.001	0.008	0.005	0.000	0.012	0.003	0.004
13.2	.012	.000	.001	.005	.024	.015	.000	.012	.013	.006
16.5	.012	.000	.001	.011	.029	.018	.000	.023	.016	.008
26.4	.016	.004	.010	.011	.027	.028	.000	.027	.017	.008
33.0	.004	.008	.000	.014	.042	.049	.023	.032	.019	.016
52.8	.012	.019	.010	.027	.066	.095	.019	.042	.022	.034
66.0	.020	.027	.011	.039	.072	.119	.044	.045	.024	.043

[1]After addition of FA, samples were heated at 60° C for 30 min to allow FA and NH_3 to react. Samples were then cooled, base added, and extracted at room temperature.

To determine if HMTA would react with picric acid, purified HMTA in dry toluene was added to the picric acid reagent. A strong color developed which indicated that HMTA reacted with picric acid. To determine if HMTA would be extracted under the standard conditions of the TMA test using 45% KOH, standard solutions of HMTA were prepared and used in the same manner as NH_4Cl solutions. The absorbancies for the HMTA samples (Table 1, column 8) were similar to the absorbancies of the samples represented by columns 5 and 7 of Table 1. Further, the absorbancies for HMTA samples were not 0 as would be expected from the literature and indicated that either HMTA was extracted by toluene and reacted with picric acid or a partial reverse reaction occurred and NH_3 was extracted and reacted with picric acid. Whether the picrate color was caused by NH_3 or by HMTA, FA did not eliminate the interference of NH_3 when 45% KOH was used. Formaldehyde gave some protection, however, if the reaction mixture was heated at 60° C for 30 min prior to the addition of 45% KOH.

Since NH_3 or HMTA was extracted by toluene at room temperature and reacted with picric acid, NH_3 was extracted at a low temperature to see if the interference could be reduced. The same standard solutions of NH_4Cl were treated as before but were extracted by the cold method. The data given in columns 9 and 10 of Table 1 showed that the absorbancies were at the same general level as the preheated samples and the presence of FA had little effect on absorbance. We conclude that 45% KOH was less effective in releasing NH_3 at −15° C than at room temperature (Table 1, compare columns 5 with 9, 6 with 10) or NH_3 was less extractable by toluene at −15° C. Although other researchers have used FA to eliminate the interference of NH_3, our data showed that FA does not tie up NH_3 under the usual conditions in the analysis for TMA. On practical grounds, the contribution of NH_3 to the TMA value would be quite low because the bases (except 45% KOH) released only a small amount of NH_3 or NH_3 was only slightly extracted by toluene. Even in advanced spoilage such as 22 mg NH_3-N/100 g flesh (66 μg N/ml), the contribution of NH_3 to the TMA value would be equivalent to 0.45 mg TMA-N/100 g flesh if extracted at room temperature with 45% KOH but only 0.10 mg TMA-N/100 g flesh if determined by the cold method.

TABLE 2.—Dimethylamine hydrochloride: the absorbancies of picrates in the trimethylamine test as affected by the three bases used and temperature of extraction. Samples were extracted for 60 s with vigorous hand shaking using 4 ml 15.9 μg DMA-N/ml, with formaldehyde (+) and without formaldehyde (0).

Temperature of extraction (°C)	25% KOH		45% KOH		50% K_2CO_3	
	1 +	2 0	3 +	4 0	5 +	6 0
−15	0.015	0.067	0.015	0.605	0.119	0.000
0	.016	.130	.031	.657	.200	.000
6	.024	.208	.053	.721	.251	.007
22	.062	.310	.157	.774	.327	.037
30	.079	.371	.361	.967	.453	.088

Reaction of DMA

Several researchers have found that DMA and TMA are not completely extracted by toluene under conditions used in the TMA test unless replicate extractions are made (Castell et al. 1974). Further, different bases resulted in different extractabilities of DMA. Accordingly, we determined the absorbancies of the picrate color using a standard solution of DMA (15.9 μg DMA-N/ml; i.e., 5.3 mg DMA-N/100 g flesh) under various conditions of the TMA test; temperature, base (K_2CO_3 and KOH), replicate extraction, and presence or absence of FA.

A standard solution of DMA·HCl in 5% TCA was extracted with and without FA by the usual methods but the temperature of extraction was varied (−15° C to +30° C) and the tubes were vigorously shaken by hand for 60 s. The extraction of DMA was strongly influenced by the base and by temperature (Table 2). In the absence of FA, the differences in reactivity of the bases in releasing DMA from the hydrochloride salt are shown in columns 2, 4, and 6 (Table 2). At −15° C, 45% KOH released about half of the DMA present, 25% KOH released 1/20th, and K_2CO_3 was unreactive and did not release DMA. The bases were more reactive at higher temperatures than at lower temperatures but had the same order of reactivity. The date also showed that, if released from the salt, DMA was extracted by toluene even at low temperatures. When FA was present however, a different order of release was evident (Table 2, columns 1, 3, and 5) and showed that FA reacted with DMA to give a product having different reactivity with the bases. The order of release (or extractability) for the product was different than for DMA, i.e., high absorbance with K_2CO_3, intermediate with 45% KOH, and low with 25% KOH. Considerable amounts of the product were extracted in the presence of FA at all temperatures in the carbonate system and would result in

a contribution by DMA of 1.69 mg N/100 g flesh to the TMA value at 22° C. In frozen flesh of gadoid fish, the DMA content might be high relative to TMA and would result in a substantial error in the TMA value unless determined at low temperatures with KOH where DMA would contribute 0.1 mg N or less.

We next studied the effects of the three bases and the presence or absence of FA on the total extractability of DMA. Similar extractions were performed by Castell et al. (1974) but these authors only considered the carbonate system with FA present. The same DMA solutions (15.9 μg DMA-N/ml) with or without FA were extracted as before but at room temperature for 15 min, i.e., 4 ml DMA solution, 10 ml toluene, 1 ml FA (or not), and 3 ml base. After removing about 7 ml toluene for drying and reacting with picric acid, the remainder of the toluene layer was carefully aspirated off, 10 ml toluene added, and reextracted. This process was repeated for a total of six extractions. In the absence of FA, DMA was released rapidly from the salt by 45% KOH, about half as fast by 25% KOH, and slowly by 50% K_2CO_3 (Table 3). If FA were present however, many extractions would be required to extract all of the DMA which, in agreement with Sprung (1940), showed that FA reacted with DMA to give TMMD. The data further showed that TMMD was relatively soluble in toluene but the extractabilities were different because each base had a different rate of reaction with TMMD, i.e., a rapid release of TMMD with K_2CO_3 and slow with 25% KOH. The possibility of each base having a different salting-out effect was eliminated when equal absorbancies were obtained if the same extractions were made with the addition of 0.5 g KCl (data not given).

The data also showed that in the carbonate method TMMD was released to the toluene phase more rapidly than DMA and explains the known interference of DMA in the presence of FA by the Dyer (1945) method. Formaldehyde might best be left out in the 50% K_2CO_3 method. The lower picrate color absorbancies in the KOH systems with FA present might also be explained by the law of mass action (equilibrium) as was done in the section on NH_3. In the equilibrium (FA + DMA $\rightleftharpoons$ TMMD) the concentrations of FA, DMA, and TMMD in the aqueous phase are dependent on the type and concentration of base. The products (FA and DMA) of the hydrolysis of TMMD would be formed at a rate dependent upon these same variables and DMA would be rapidly removed from the aqueous phase in the KOH systems because of the rapid extraction of DMA by toluene. Since the absorbancies in the KOH systems were relatively low in the presence of FA, the concentration of DMA from the hydrolysis of TMMD must have been low. In the carbonate system however, DMA from TMMD was slowly released from the aqueous phase into the toluene layer. Apparently a low concentration of DMA existed in the equilibrium formed in the carbonate system and favored the extraction of TMMD by toluene. It is likely that both TMMD and DMA were extracted by toluene at rates that depend on the base and temperature used.

To further study the extraction of TMMD, the same multiple extractions described for DMA were made using purified TMMD in 5% TCA but at a slightly lower concentration (15.0 μg TMMD-N/ml). The absorbancies of the TMMD-picrates (Table 4) were nearly the same as the absorbancies of the DMA-picrates (Table 3). The similarity of data between DMA and TMMD inferred again that FA and DMA react to give TMMD. The addition of FA forced the reaction toward TMMD where the type and concentration of base con-

TABLE 3.—Dimethylamine hydrochloride: the absorbancies of picrates in multiple extractions in the trimethylamine test as affected by the three bases used. Samples were extracted for 15 min at room temperature using 4 ml 15.9 μg DMA-N/ml, with formaldehyde (+) and without formaldehyde (0).

Extraction number	25% KOH		45% KOH		50% K_2CO_3	
	1	2	3	4	5	6
	+	0	+	0	+	0
1	0.064	0.416	0.184	1.022	0.498	0.03
2	.042	.175	.160	.204	.273	.02
3	.049	.125	.149	.017	.195	.01
4	.040	.057	.114	.000	.114	.02
5	.049	.036	.117	.000	.074	.02
6	.049	.015	.092	.000	.051	.02

TABLE 4.—N N N'N'-tetramethylmethanediamine: the absorbancies of picrates in multiple extractions in the trimethylamine test as affected by the three bases used. Samples were extracted for 15 min at room temperature using 4 ml 15.0 μg TMMD-N/ml, with formaldehyde (+) and without formaldehyde (0).

Extraction number	25% KOH		45% KOH		50% K_2CO_3	
	1	2	3	4	5	6
	+	0	+	0	+	0
1	0.051	0.308	0.193	0.882	0.417	0.041
2	.038	.198	.160	.180	.277	.041
3	.046	.123	.142	.028	.185	.044
4	.036	.067	.122	.002	.126	.048
5	.039	.031	.090	.000	.081	.028
6	.046	.022	.073	.000	.059	.025

trolled the degree of retention of TMMD in the aqueous phase or its release to the toluene phase. The use of 1 ml 3.7% FA and 4 ml 15.9 μg DMA-N/ml results in a large excess of FA, about 500 times over that required (1 FA to 2 DMA). Consequently, in the absence of added FA where only the stoichiometric amount of FA was present from TMMD, an equilibrium was established in the KOH systems that favored the formation of DMA and its rapid extraction by toluene. A different equilibrium was formed in the K_2CO_3 system that favored the release of TMMD and extraction by toluene.

Extraction of TMA

The extraction of TMA under various conditions of base, temperature, and FA was examined. A standard solution of TMA·HCl in 5% TCA was prepared (15.9 μg TMA-N/ml, i.e., 5.3 mg TMA-N/100 g). This concentration was chosen as it is near the point of unacceptable quality for fish. In the carbonate method (Table 5), the extraction of TMA was highly dependent upon temperature and would result in a lack of precision unless the temperature was controlled as suggested by Hashimoto and Okaichi (1957). Absorbancies were not as dependent upon temperature in the 25% KOH method as with K_2CO_3 and were nearly independent of temperature with 45% KOH. The slightly lower absorbancies with FA present than if not present might be caused by an impurity of DMA or an interference from FA even though FA would not be expected to react with a tertiary amine. As stated in the section on DMA, FA might best be left out in the carbonate method, i.e., only 10% less TMA was extracted than was extracted in the 45% KOH method.

To determine the conditions for maximum extractions of TMA, the same multiple extractions were done as with DMA. In the 45% KOH test (Table 6), 97% of the TMA was removed in the first extraction and the remainder was removed in the second extraction. The first, second, and third extractions removed 80, 17, and 3% with 25% KOH and removed 72, 21, and 6% with 50% K_2CO_3. Standard curves are assumed to compensate for constant experimental errors such as slightly less than 100% extraction of TMA, but the reliability of the data would be questionable with the low recoveries reported here for 25% KOH and 50% K_2CO_3. Neither do standard curves compensate for variable errors such as the observed strong dependence on temperature of the extraction of TMA in the 25% KOH and 50% K_2CO_3 methods (Table 5).

TABLE 5.—Trimethylamine hydrochloride: the absorbancies of picrates in the trimethylamine test as affected by the three bases used and temperature of extraction. Samples were extracted for 60 s with vigorous hand shaking using 4 ml of 15.9 μg TMA-N/ml, with formaldehyde (+) and without formaldehyde (0).

Temperature of extraction (°C)	25% KOH		45% KOH		50% K_2CO_3	
	1 +	2 0	3 +	4 0	5 +	6 0
−17	0.685	0.854	1.312	1.402	0.286	0.682
0	.921	1.099	1.366	1.412	.630	1.027
6	1.050	1.138	1.378	1.391	.722	1.095
21	1.136	1.235	1.373	1.350	1.013	1.218
30	1.198	1.269	1.408	1.420	1.150	1.303

TABLE 6.—Trimethylamine hydrochloride: the absorbancies of picrates in multiple extractions in the trimethylamine test as affected by the three bases used. Samples were extracted for 15 min at room temperature using 4 ml 15.9 μg TMA-N/ml, with formaldehyde (+) and without formaldehyde (0).

Extraction number	25% KOH		45% KOH		50% K_2CO_3	
	1 +	2 0	3 +	4 0	5 +	6 0
1	1.113	1.223	1.384	1.403	0.987	1.245
2	.233	.159	.050	.033	.282	.130
3	.044	.020	.000	.001	.079	.009
4	.003	.005	.000	.000	.016	.003

Comparative Analyses Using Fish Flesh

Walleye pollock, *Theragra chalcogramma*, were held in slush-ice for 9 d and filleted. Twelve separate TCA extractions were made on a composite sample of the ground flesh. Each extract was analyzed in duplicate by each of the three TMA methods and the cold method. Portions of the extracts were neutralized and analyzed for DMA by Dowden's 1938 method, modified slightly by increasing the time of extraction to 15 min on the modified mechanical shaker.

All methods (Table 7) resulted in similar standard deviations but the TMA values were higher in the K_2CO_3 method than in the KOH methods and the cold method of extraction gave the lowest value. The absorbancy data at 22° C of Table 2 can be used to approximate the degree of contribution of DMA to the TMA values in Table 7. The flesh contained 2.25 mg DMA-N/100 g (6.75 μg/ml) and would contribute different amounts to the TMA value according to the method of analysis employed. The data of Table 2 for K_2CO_3 (0.327 *A* at 22° C using 15.9 μg DMA-N/ml) are equivalent

TABLE 7.—Trimethylamine content in mg TMA-N/100 g flesh from 9-d-old walleye pollock using four methods of analysis.

Extract number	Room temperature extraction			−15° C extraction
	25% KOH	45% KOH	50% K_2CO_3	45% KOH
1	9.52	9.84	10.42	9.18
2	9.73	9.76	10.27	9.14
3	9.55	9.78	10.18	9.08
4	9.66	10.01	10.28	8.84
5	9.53	9.92	10.34	8.84
6	9.69	10.07	10.25	9.10
7	9.51	9.93	10.39	9.28
8	9.56	9.78	10.28	8.97
9	9.49	9.82	10.22	9.18
10	9.65	9.79	10.21	8.91
11	9.65	9.75	10.22	9.11
12	9.55	9.82	10.39	9.11
Mean	9.59	9.85	10.29	9.06
SD	.08	.10	.08	.14

to 0.139 A for 6.75 μg DMA-N/ml by a simple ratio, i.e., 0.327A/(15.9 μg DMA-N/ml):X/(6.75 μg DMA-N/ml). An equivalent TMA value was calculated to be 0.75 mg TMA-N/100 g flesh from Equations (3) and (5). If corrected for DMA, the TMA value from Table 7 (K_2CO_3) would be 10.29 − 0.75 = 9.54 mg TMA-N/100 g flesh. Similar calculations for the 25 and 45% KOH methods gave corrected values of 9.45 and 9.59 mg TMA-N/100 g flesh. The small contribution of DMA at −15°C (0.015 A) would be 0.05 mg TMA-N/100 g flesh and give a corrected value of 9.01 for the cold method. The TMA values obtained by the three methods of analysis were in good agreement if corrected for DMA. The cold method of extraction gave slightly lower and more accurate values than the other methods. Cold extraction reduced the release and extractability of numerous other interfering substances discussed by Dyer (1945).

Extraction of Fish Flesh with Added TMA and DMA

To determine the recovery of TMA and the interference of DMA, varying amounts of both were added to blended flesh of Pacific cod, *Gadus macrocephalus*, extracted with TCA in the usual way and analyzed for TMA content by four methods. The sample of flesh contained 3.25 mg DMA-N/100 g by Dowden's method (1938). The amount of amine added, the resulting TMA value, and the percentage of the theoretical value (recovery) by each method of analysis are given in Table 8. The TMA values of cod flesh with added TMA (3, 6, 9, and 12 mg) resulted in similar recoveries of TMA by all methods. If 5, 15, 30, and 50 mg DMA were added to the blended flesh, however, the TMA values were unacceptably high by the 50% K_2CO_3, 25% KOH, and 45% KOH methods. The cold method gave acceptable values although the addition of 50 mg DMA-N increased the TMA value from 1.59 to 2.12, i.e., 133% of theory. If the same quantities of DMA were added plus a small amount of TMA (3 mg), only the cold method gave acceptable TMA values. The other methods were strongly influenced by the presence of DMA. However, if larger amounts of TMA were added (12 mg), along with DMA, the influence of DMA was reduced considerably and the 25% KOH and cold methods gave acceptable results.

All methods gave about equal recovery of added TMA provided the DMA content was low. Trimethylamine values by the three published methods were strongly influenced by the relative

TABLE 8.—Trimethylamine values in mg TMA-N/100 g flesh of Pacific cod as affected by different methods of analysis when varying amounts of the TMA·HCl and DMA·HCl salts were added to the flesh before extracting with TCA.

Levels of TMA and DMA added	25% KOH		45% KOH		50% K_2CO_3		Cold method	
	TMA-N (mg)	Recovery (%)	TMA-N (mg)	Recovery (%)	TMA-N (mg)	Recovery (%)	TMA-N (mg)	Recovery (%)
Sample, as is	1.65		1.94		2.36		1.59	
3 mg TMA	4.81	103	5.17	105	4.89	91	4.81	105
6 mg TMA	7.34	96	8.28	104	7.39	88	8.12	107
9 mg TMA	11.62	109	10.71	98	11.39	100	11.32	107
12 mg TMA	13.94	102	15.23	109	17.04	119	14.90	110
5 mg DMA	2.00	121	2.83	146	3.79	161	1.72	108
15 mg DMA	2.47	150	4.24	219	6.32	268	1.77	111
30 mg DMA	3.18	193	5.89	304	10.16	431	1.89	119
50 mg DMA	3.83	232	8.09	417	14.46	613	2.12	133
3 mg TMA+5 mg DMA	5.21	112	6.14	124	6.84	128	4.60	100
3 mg TMA+15 mg DMA	5.70	123	7.59	154	9.25	173	4.81	105
3 mg TMA+30 mg DMA	6.35	137	9.74	197	11.87	221	4.97	108
3 mg TMA+50 mg DMA	7.78	167	13.10	265	16.35	305	4.98	108
12 mg TMA+5 mg DMA	14.48	106	16.42	118	19.39	135	15.24	112
12 mg TMA+15 mg DMA	14.88	109	16.71	120	19.83	138	15.34	113
12 mg TMA+30 mg DMA	14.93	109	17.90	128	21.17	147	15.16	112
12 mg TMA+50 mg DMA	15.79	116	19.72	141	24.27	169	15.19	112

amounts of TMA and DMA in the sample. Only the cold method gave TMA values that were nearly independent of the DMA content of all levels of DMA and TMA. If methods other than the cold method are used to analyze for TMA, the history of the fish and sample storage should be known or the DMA content should be determined separately.

RECOMMENDED PROCEDURES

Extraction Procedure for Fish Flesh

Blend a thoroughly mixed composite sample of fish flesh (75 g) with 90 ml of 8.2% (weight/volume) TCA for 5 min at high speed in a Vertis blender. Pour contents of blender jar into a 150 ml medium porosity sintered glass funnel and filter under vacuum. To prevent foaming and plugging of filter, clamp off the suction line after filtering starts and briefly open when required. Reextract residue with 70 ml of 5% TCA for 2 min and filter into the same filter flask and rinse with 5% TCA from a wash bottle. Quantitatively transfer the combined filtrates and washings to a 250 ml volumetric flask and dilute to the mark with 5% TCA. The extract (4 ml) is used in the TMA analysis without dilution but, if required, 4 ml of a diluted extract is used rather than smaller volumes of extract.

Cold Method of Analysis for TMA

Add 4 ml samples of standard solutions of TMA·HCl in 5% TCA or 5% TCA extracts, 10 ml toluene, and 1 ml of 3.7% FA to 25 × 150 mm screw top test tubes. Allow to stand for 5 min then place tubes in an ice-water bath in an effort to avoid the possible yellow color caused by the addition of concentrated KOH (Castell et al. 1974). When completely chilled, add 3 ml 45% KOH and tightly seal tubes, invert twice, and place in a mixture of salt and precooled saturated brine-ice at −15° C. Use a pump or stirring motor to maintain constant temperature by circulating the brine through the salt, brine-ice mixture. After 2 min, remove the test tubes and shake vigorously by hand for 15 s and replace in the cold bath for 2 min. Repeat this procedure three times for a total of 60 s of vigorous hand shaking. After settling (almost immediately), transfer about 7 ml of the toluene layer to clean dry 18 × 150 mm test tubes and dry with about 0.5 g anhydrous Na_2SO_4 by swirling (Vortex Mixer). After drying, remove 5 ml and add to 5 ml of 0.02% picric acid in dry toluene. Determine the absorbance at 415 nm using 1 cm standard silica cells and a Gilford modified Beckman D.U. spectrophotometer. Determine the blank in the same manner but use 4 ml TCA. Calculate the TMA content in mg TMA-N/100 g from the absorbance and Equations (4) and (5).

SUMMARY

Although NH_3, DMA, and other amines contribute to the TMA value, the TMA content of some marine fish, especially gadoid species, is accepted internationally as an index of spoilage. Variations in the conditions of the three methods used to analyze for TMA were studied to determine the best condition to extract TMA and to reduce the extraction of HN_3, DMA, and other amines. We found that NH_3 was not tied up by FA as suggested in the literature but has little affect on the TMA value of fish even in advanced spoilage. The amount of DMA extracted was strongly dependent on the temperature of extraction, the base used, and the presence or absence of FA. Formaldehyde and DMA reacted to form a compound that was rapidly extracted by 50% K_2CO_3 and very slowly by 25% KOH. If DMA and TMMD were extracted, the absorbancies were nearly the same which infers that the compound formed from FA and DMA was TMMD. The amount of TMA extracted was strongly dependent on the temperature of extraction when 25% KOH or 50% K_2CO_3 was used as the base but nearly independent when 45% KOH was used. A cold method of extraction (45% KOH and −15° C) was developed that essentially eliminated the contribution of DMA to the TMA value. Trimethylamine was determined in spoiled fish flesh by the cold method and the three other methods. Standard deviations were similar for all four methods. The K_2CO_3 method gave the highest value and the cold method gave the lowest value. If varying amounts of TMA and DMA were added to Pacific cod flesh and analyzed by the three published TMA methods, the recovery of TMA and interference from DMA was strongly influenced by the relative amounts of TMA and DMA present. Relative to the other methods, the cold method gave TMA values that were independent of the presence of DMA or the relative amounts of DMA and TMA. We recommend that the cold method be used because it extracts most of the TMA (97%), gives good recovery of added

TMA, is nearly independent of DMA content, and is not affected by other amines or NH_3.

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PERCENTAGE OF STARVING NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE IN THE SEA AS ESTIMATED BY HISTOLOGICAL METHODS

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ABSTRACT

The proportion of starving larvae of northern anchovy, *Engraulis mordax*, was estimated for the Southern California Bight in March 1977 from histological examination of larvae for 64 1 m net tow samples. The number of larvae in the tows varied from 0 to about 400. Approximately 6 per tow were sectioned and examined with the light microscope. Twenty-six specimens were identified as emaciated from anomalies of the trunk musculature and digestive tract. Some of the emaciated larvae occurred as isolated cases at widely scattered locations, but most were from a few nearshore tows, indicating "patches" of starving larvae. Temperature and plankton volume data indicate that the patches were associated with fluctuating environmental conditions. The samples indicate that about 8% of northern anchovy larvae in the Southern California Bight were starving.

One of the goals in investigations of pelagic fish stocks is that of predicting how large year classes will be at the time they are recruited to the fishery. One of the primary approaches to this problem has been the estimation of larval mortality rates based on abundance estimates from egg and larval surveys. While such surveys will probably continue to be the most reliable source of information on abundance at early ages, the high costs and time delays in processing samples are reasons for seeking alternative approaches (Hunter 1976b). Recently, Lasker (1975, in press) has developed a promising index based on availability of food in concentrations suitable for survival of early feeding stages of the northern anchovy, *Engraulis mordax*.

This study reports another approach that could provide an independent prediction of year class strength for the northern anchovy; namely, estimation by histological methods of the proportion of larvae in the sea showing symptoms of starvation. Since level of mortality in a population is likely to be some function of the proportion of larvae observed to be starving, the proportion, if based on adequate sampling, could be an indicator of ultimate year class success.

Condition factor (Blaxter 1971), chemical indices (Ehrlich 1974), morphometric analyses (Shelbourne 1957; Nakai et al. 1969; Ehrlich et al. 1976; Theilacker 1978), and histological analyses (Umeda and Ochiai 1975; O'Connell 1976; Theilacker 1978) have all been used with some success to characterize the starving condition in larvae of various marine species, in most cases under controlled laboratory conditions. The histological approach differs from the others in that the criteria of starvation are based on qualitative changes in the character of cells and tissues, not on quantitative measurements. Histological criteria developed earlier for northern anchovy larvae starved in the laboratory (O'Connell 1976) were the principal guidelines for evaluating the condition of ocean-caught larvae in this study.

METHODS

In March 1977, 64 net tows were taken over a 12-d period from the NOAA ship *David Starr Jordan* to obtain northern anchovy larvae for histological study. Almost half of the tows were taken between 2 and 10 mi (3.7-18.5 km) from the coast, most were near Newport Beach, Calif., where northern anchovy eggs and larvae were abundant, but some were much farther offshore. A surface temperature was taken by bucket thermometer at each net tow station.

Net tows were taken with a 1 m plankton net on which the cod end was a cylindrical Plexiglas[2]

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bucket (length 30.5 cm, diameter 10 cm) that could be removed quickly. Tows were of short duration to minimize the time larvae would be under stress during capture. The net was let out at a fast steady rate to a depth of 20 m, and then retrieved at a moderate rate. The mean tow time was 3 min (SD = 40 s).

The net drained rapidly as it was hauled out of the water, leaving the cod end cylinder filled with water containing a light to moderate amount of plankton. The contents of the cylinder were immediately poured into a small sieve made of 0.505 Nitex mesh netting, and the sieve was then suspended in Bouin's fluid to fix the concentrated plankton. The total elapsed time from start of tow, when the plankton net first entered the sea surface, to submergence in Bouin's averaged 5 min, 8 s (SD = 1 min, 9 s). After the initial fixation, about 10 or 15 min, the sample was transferred from the sieve to a jar of fresh Bouin's, and this was replaced by 70% ethyl alcohol 2 or 3 d later.

In carrying out the above procedure the inside of the plankton net was not washed down after retrieval until the cod end containing the sample had been removed. After the cod end was removed, the inside of the net was hosed down thoroughly in preparation for the next tow.

Subsequent to the cruise, all northern anchovy and other fish larvae were sorted out of the samples and counted. From those tows containing only a few northern anchovy larvae, all were set aside for sectioning. From those tows containing many larvae, about half a dozen were chosen for sectioning. The number was approximately doubled for a few samples of special interest, e.g., offshore banks. Specimens were picked at random by putting all northern anchovy larvae from a given tow in a shallow, wide-mouth container and repeatedly dipping with a vial as the contents were swirling slowly. During this procedure small specimens with obvious yolk sacs were rejected because they represented nonfeeding larvae not yet vulnerable to starvation.

The total number of larvae selected for sectioning was 318. Standard length was measured with an ocular micrometer, then each specimen was imbedded in paraffin, sectioned serially as close to the sagittal plane as feasible, and stained in Harris' hematoxylin and eosin-phloxine B. Prior to microscope examination the mounted specimens were put in random order with their identities concealed.

Histological criteria similar to those diagnostic for laboratory starved larvae were readily established for ocean-caught larvae by preliminary examination of a few dozen (unidentified) specimens, after which all ocean-caught larvae were classified as to condition. Under Results, the histological indications of condition are described first, and then the classification of larvae is examined in relation to other variables, i.e., standard length, geographical distribution, temperature, and plankton volume.

RESULTS

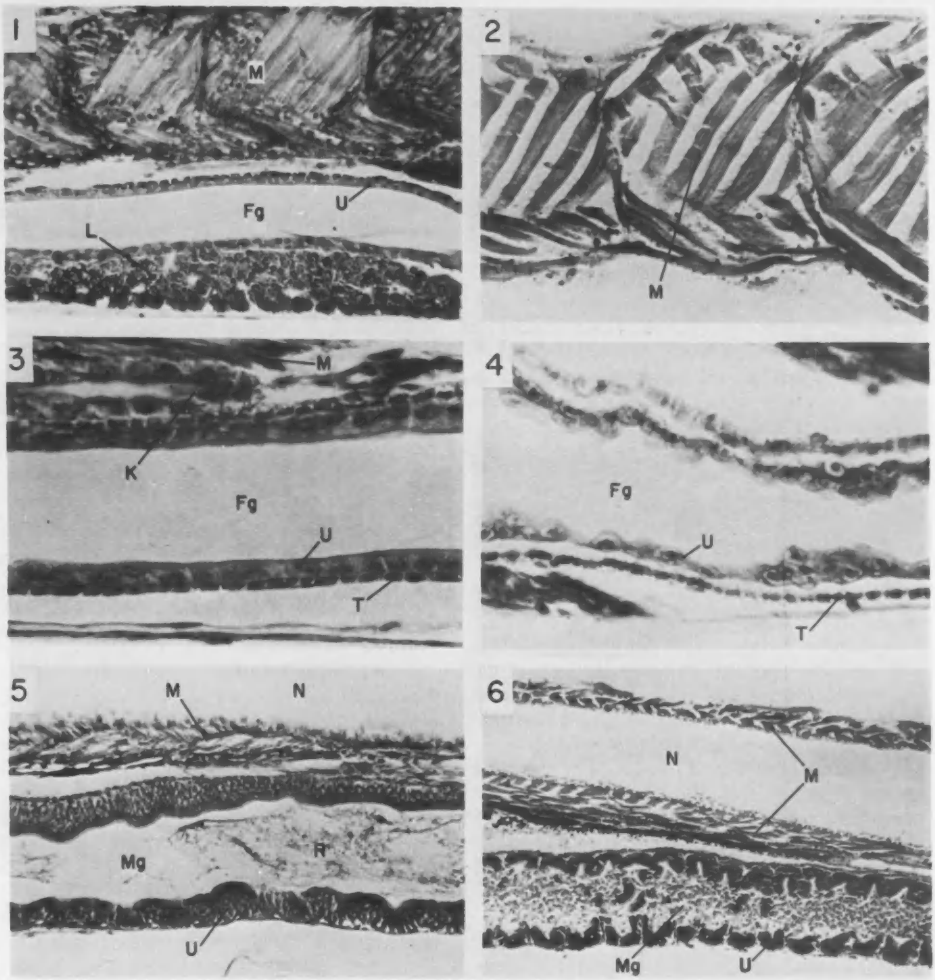
Histological Characteristics of Condition

O'Connell (1976) found the most noticeable effects of artificial starvation of northern anchovy larvae just beyond yolk absorption (3-5 mm) to be cellular dissociation with loss of zymogen in the pancreas, separation and hyalinization of trunk muscle fibers, and shrinkage of the notochord. In the ocean-caught material examined in the present study, specimens ranging from 2.5 to 10 mm showed anomalies in the trunk musculature and notochord, and occasionally also in the pancreas, that closely resembled the effects of starvation in the laboratory material. These larvae almost always showed, in addition, certain irregularities in the histology of the foregut and the midgut that were more striking than effects seen in the digestive tracts of artificially starved larvae.

Trunk Musculature

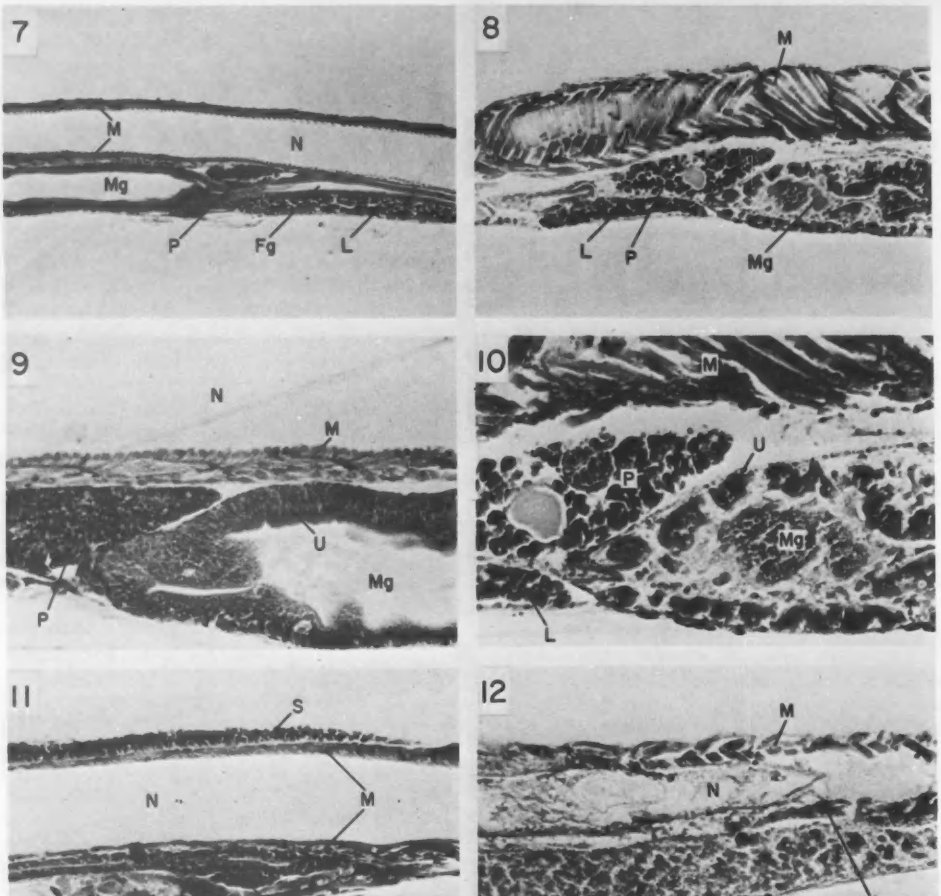
The trunk musculature in the majority of larvae showed good integrity and texture, forming a compact, solid sheet over the lateral surfaces of the notochord, with evident intermuscular matrix tissue and only occasional small separations (Figure 1). The notochord in such larvae generally had a smooth profile and was rarely separated from the musculature. In some specimens, however, the muscle fibers were noticeably separated from each other throughout, indicating an anomalous condition. In the more extreme cases (Figure 2) the fibers were widely separated with degraded fibril clarity, and matrix tissue was greatly reduced. In such specimens the notochord was also irregular in profile, imparting a "lumpy" shape to the trunk of the animal as a whole.

Degraded musculature, of course, might be the result of some process other than starvation. One possibility is capture myopathy, which has been



FIGURES 1-6.—Histological comparisons of healthy (left) and emaciated (right) northern anchovy larvae. All sections are approximately sagittal. 1) The trunk musculature, cut tangential to the body surface, forms a solid sheet. The foregut mucosa is composed of uniform cuboidal cells. 6.1 mm SL; 250×. 2) The trunk musculature, cut tangentially, shows widely separated fibers. 8.5 mm SL; 250×. 3)The foregut mucosa is composed of uniform thick cuboidal cells. 7.0 mm SL; 630×. 4) The foregut is irregular and the cells of the mucosa are diminished in size. 6.1 mm SL; 630×. 5) The mucosa of the midgut shows good integrity and organization, and the lumen contains moderate food residue. 6.3 mm SL; 250×. 6) The midgut is filled with disassociated cellular debris and the mucosa is fragmentary. Separated trunk muscle fibers are also visible. 8.5 mm SL; 250×. Symbols: Fg, foregut; K, kidney; L, liver; M, trunk muscle; Mg, midgut; N, notochord; R, food residue; T, transverse muscle coat of digestive tract; U, mucosa.

reported for a number of ungulates, primates, and birds (Harthoorn 1977) and in the swordfish, *Xiphias gladius* (Tibbo et al. 1961). The outstanding symptom is degeneration of skeletal muscle, presumably from acidemia from overexertion during intense flight and struggle in capture. Though the possibility cannot be entirely dismissed, capture myopathy seems an unlikely cause of the



FIGURES 7-12.—Histological comparisons of healthy (left) and emaciated (right) northern anchovy larvae.—Continued. 7) The trunk muscles cut in cross section above and below the notochord are compact. The foregut and midgut have mucosa of good thickness and integrity. 5.5 mm SL; 100×. 8) Trunk muscles are separated and uneven, the midgut is filled with disassociated cellular material, and the pancreas is severely disassociated. 5.5 mm SL; 100×. 9) Portions of the midgut, the pancreas, and the trunk musculature below the notochord all show good integrity. 5.0 mm SL; 250×. 10) Enlargement of Figure 8 for comparison of pancreas to that in Figure 9. 250×. 11) The foregut is regular and the trunk muscles are compact. The foregut is not yet expanded, and the midgut is not visible in the section. The remnant of the yolk sac, primarily periblast tissue, is prominent. 2.5 mm SL; 250×. 12) The midgut is a solid mass of necrotic debris. The notochord and trunk muscles are collapsed and irregular. The kidney is necrotic. 2.2 mm SL; 250×. Symbols: Fg, foregut; K, kidney; L, liver; M, trunk muscle; Mg, midgut; N, notochord; P, pancreas; S, spinal cord; U, mucosa; Y, yolk.

muscle deterioration observed in the northern anchovy larva. It is essentially a phenomenon of protracted struggle in large animals. In the case of the northern anchovy larvae, time and physical manipulation were minimized in capture.

Depletion of tissues arising from starvation

seems a more likely cause of muscle deterioration. Love (1974), in summarizing depletion in (adult) fishes, states that ". . . when fish are starved the lipid reserves . . . decrease to a certain point beyond which the muscle protein is mobilized. As the protein decreases, the water increases, and this change is mainly brought about by shrinkage of the cells and a corresponding increase in the fluid between them." In conjunction with these findings it had been shown that extracellular spaces appeared in the musculature of Atlantic cod, *Gadus morhua* (Love et al. 1968), and American plaice, *Hippoglossoides platessoides* (Templeman and Andrews 1956). Deterioration of the musculature was a prominent effect following artificial starvation of early postyolk-sac northern anchovy larvae (O'Connell 1976) and of jack mackerel, *Trachurus symmetricus*, larvae (Theilacker 1978). Deterioration of musculature during starvation has also been observed in larval herring, *Clupea harengus*, and plaice, *Pleuronectes platessa* (Ehrlich et al. 1976).

Digestive Tract

In most larvae the long foregut was straight with a uniform lumen and a smooth surfaced mucosa of cuboidal or thick squamous cells (Figure 3; see also Figures 1 and 7). The foregut was considered anomalous if the profile was noticeably irregular in sagittal view. The mucosa usually also showed some variation in cell thickness and shape. In the more extreme cases the mucosa cells tended to be reduced to little more than the nucleus (Figure 4), and the lumen sometimes contained a few sloughed cells.

The midgut varied greatly in appearance, depending on the degree of longitudinal folding and transverse ridge development and on the plane of a particular section. Nevertheless, in most specimens a substantial lumen, sometimes containing food, and a simple mucosa of low columnar cells could be traced (Figures 5, 7, 9). Although the infranuclear portions of the cells were often narrowed and slightly separated, the supranuclear portions were always well joined.

The midgut was judged anomalous when little or no lumen could be traced, or when the traceable lumen contained a considerable bulk of loose nuclei and necrotic cellular debris, and the mucosa proper was fragmenting (Figures 6, 8, 10). In the worst case the midgut was a homogeneous mass of necrotic debris enclosed in only a basement membrane, with no trace of either lumen or mucosa (Figure 12). This specimen, which happened to be the smallest examined, also showed a severely collapsed notochord and degenerate musculature. The degree of organ development, including fully pigmented eyes, indicated that it had shrunken. Healthy specimens of comparable size, which still had unpigmented eyes, showed good notochord and musculature, and often a sizable remnant of the yolk sac (Figure 11). Shrinkage has been shown in laboratory starved larvae of both the Atlantic herring (Blaxter and Hempel 1963) and the northern anchovy (O'Connell 1976; O'Connell and Raymond 1970).

Whereas the muscle and foregut anomalies are at least logically acceptable as consequences of inadequate nourishment, interpretation of the midgut anomaly is problematical. In artificially starved northern anchovy larvae the midgut showed thinning and increased separation of cells, and the loss of some cells (O'Connell 1976), but not strong contraction followed by general fragmentation and necrosis of the mucosa as seen in some of the ocean-caught specimens. It may be, of course, that the symptoms were different because the laboratory and ocean situations were different. Laboratory animals were starved without ever having an opportunity to feed, whereas the oceanic larvae showing symptoms undoubtedly did have the opportunity to feed. Most in fact had processed food through the digestive tract, as indicated by the presence of supranuclear inclusion bodies in the mucosa cells of the hindgut, though the hindgut and the inclusion bodies were sometimes in a state of disintegration. Such inclusion bodies were never found in laboratory specimens deprived of food from time of hatching (O'Connell 1976).

Contraction and congestion resembling that seen in the midguts of the emaciated northern anchovy larvae from the ocean have been described for some other fishes, but they can be symptomatic of disease as well as of starvation. *Clupea harengus* larvae of 9-13 mm, for example, are vulnerable to a nematode that grows in the body cavity and deforms the gut, often resulting in occlusion of the lumen that blocks food intake and/or defecation (Margolis 1970). There are other nematodes whose larvae attack the gut walls of certain fishes, causing inflammatory and degenerative changes, including localized necrosis and infiltration of abundant lymphocytes (Margolis 1970). There are also protozoans, such as

Nosema anomala, which invade the intestinal wall of the young of the threespine stickleback, *Gasterosteus aculeatus*, and generate hypertrophied cells filled with its vegetative and reproductive stages (Lom 1970). Certain viral diseases produce degenerative changes that include necrosis and sloughing of intestinal epithelium (Yasutake 1975). On the other hand, starvation of immature salmon cause, among other things, marked atrophy of the stomach with degeneration of the epithelium, which ". . . could presumably be used for nourishment" (Love 1974). Starvation of

TABLE 1.—Numbers of northern anchovy larvae and other data by net tow for March 1977, off southern California. Number emaciated and standard length pertain only to sectioned larvae. See Figures 13 and 14 for tow locations.

Tow	Date	Hour	Temperature (°C)	Plankton volume (ml)	Number of Larvae		Mean standard length	Number emaciated		
					In tow	Sectioned		Severe	Moderate	Incipient
1	17	1530	13.2	1	0					
2		1750	13.8	5	9	6	4.6			
3		2210	13.5	4	33	7	4.0	1		
4	18	0825	14.2	2	9	5	5.0			
5		1035	14.5	2	9	5	4.9			
6		1440	14.7	3	14	6	6.4			
7		1910	14.7	3	68	6	5.4			
8		2340	14.8	2	47	6	4.7			
9	19	0350	13.7	3	54	6	4.5	3	1	
10		1010	15.2	4	7	7	4.9	3		1
11		1215	15.6	3	2	2	3.9		1	
12		1550	15.5	1	32	6	5.1			
[1]13		1600		8	[2]200	6	5.2			2
14		2215	14.6	11	43	6	4.7			
15	20	0005	13.4	4	24	10	6.7	4	1	2
16		0735	13.6	4	58	6	4.7			
17		1155	14.0	10	20	7	5.5			
[1]18		1205		3	15	6	4.2			
19		2045	15.0	7	70	6	5.5			
20	21	0005	14.9	4	65	7	6.5	4	2	1
21		2045	14.2	21	[2]400	6	5.0			1
22	22	1020	14.2	7	16	6	5.7			
23		2255	13.6	32	[2]350	7	6.0			
24	23	0945	14.6	6	40	6	4.2			
[1]25		0955		10	54	6	4.4			
26		1110	14.7	3	5	5	4.4			
27		2045	14.1	12	180	6	4.9			
28		2315	13.4	7	56	5	5.4		1	
29	24	1020	14.7	14	62	6	5.3			
[1]30		1030		8	67	7	5.3			
31		1440	13.7	7	8	6	5.4			1
32		1915	14.8	11	[2]200	6	4.7			1
33	25	0120	13.8	35	[2]300	6	4.9			
34		1550	13.1	14	97	7	4.8			
[1]35		1555		5	22	6	5.7			
36		2310	13.4	6	122	7	6.9			
37	26	0140	13.1	38	[2]250	5	7.1			
38		0345	12.7	10	19	6	6.6			
39		0550	12.3	33	4	4	12.5			
40		0730	12.8	17	0					
[1]41		0740		29	0					
42		0927	12.7	106	1	1	8.0			
43		1300	14.4	4	1	1	5.9			
[1]44		1325		21	1	1	12.2			
45		1620	14.1	1	0					
[1]46		1630		12	1	1	8.5			
47		1745	14.5	7	0					
48		2030	14.2	13	2	2	10.6			
49		2205	14.2	21	2	2	9.3			
50		2345	14.3	15	3	3	7.2		1	
51	27	0120	13.8	19	2	2	8.2			
52		0240	13.2	29	16	16	12.3			
53		0410	13.2	42	35	15	11.0		1	
54		0645	14.2	7	0					
55		1340	14.5	10	0					
56		1450	14.6	20	0					
57		1600	14.5	7	0					
[1]58		1610		30	0					
59		1839	14.1	27	5	4	9.8	1		2
60		2115	14.0	17	3	3	12.8		1	
61		2330	13.8	12	1	1	11.7			
62	28	0145	14.4	15	11	7	9.4			
63		0415	15.2	5	42	14	7.1			
64		0640	15.2	2	22	15	6.9	1		

[1]Taken at same location as preceding tow at almost twice the depth.
[2]Number estimated from count of a substantial fraction.

mummichog, *Fundulus heteroclitus*, up to 8 days resulted in a decrease in the quantity of lipid droplets in cells of the digestive tract and contraction of the intestine such that the lumen was small, sometimes scarcely traceable (Ciullo 1975). While these considerations suggest that disease could be the cause of the midgut anomaly present in certain of the ocean-caught northern anchovy larvae, starvation is the more tenable explanation because there was no evidence of parasites or pathogens in the hematoxylin- and eosin-stained specimens, and other anomalies in these specimens were consistent with demonstrated effects of starvation.

Other Organs

Deterioration was sometimes evident in other organs, particularly in the specimens with the most severe anomalies in the musculature and digestive tract. The pancreas and liver, for example, showed good integrity in most larvae (Figures 1, 9), but some showed an unusual degree of dissociation in these organs (Figures 8, 10), and in a few, both organs had undergone considerable lysis. The kidney ducts were intact in all specimens, but in a few the cells of the ducts were unusually thin, or necrotic (Figure 12). In several the mantle layer of the brain showed poor integrity, perhaps from a reduction of neuroglia.

Classification of Larvae

During the course of microscope examination, each larva was designated healthy, incipient emaciation, moderate emaciation, or severe emaciation. The three classes pertaining to larvae with anomalies are not rigorous, but they imply the following: incipient, slight looseness of the trunk muscles; moderate, obvious separation of the trunk muscle fibers, some irregularity of the notochord and possibly the foregut, strong contraction of the midgut, and sometimes a high incidence of hypertrophic cells in the midgut mucosa; and severe, obvious separation and hyalinization, and sometimes disarray, of the muscle fibers, notable irregularity in the profile of the notochord and foregut, depletion of foregut muscosa cells, and fragmentation of midgut mucosa, with a central core of dissociated and necrotic cellular debris. Of the 318 larvae sectioned, 26 were classified as severely or moderately emaciated, and another 11 were classified as incipient. These are listed by net tow in Table 1 along with the raw data for all tows. The larvae classified as incipient are included with the healthy rather than with the emaciated or "starving" group in the sections that follow.

Relation of Emaciated Larvae to Other Variables

Standard Length

Emaciated larvae were all <10 mm SL and were distributed almost proportionately over the range 2-10 mm SL (Table 2). Larvae classified incipient were similarly distributed. In the lowest size category, 2.1-4.0 mm SL, only half of the 46 larvae examined had exhausted their yolk and become vulnerable to starvation. The emaciated individuals were part of this contingent. The absence of emaciated larvae in the categories above 10 mm SL may be a chance result of the relatively fewer numbers of larger larvae present in the tows, but there may also be some actual reduction in starvation effects at this size because of increasing lipid reserves with growth (Love 1974).

TABLE 2.—Standard length distribution of the northern anchovy larvae sectioned and examined and of those classified as emaciated or incipient.

Standard length	Number examined	Number emaciated	Number incipient
2.1- 4.0	46	6	3
4.1- 6.0	137	8	3
6.1- 8.0	60	8	3
8.1-10.0	30	4	1
10.1-12.0	26		1
12.1-14.0	14		
14.1-16.0	3		
16.1-20.0	3		

Geographical Distribution

More than half of the tows were spread over a large offshore area where abundance of northern anchovy larvae was generally low (Figure 13, Table 1) and where samples from six tows each contained a single emaciated larva. The remainder of the tows occurred in an area of a few hundred square miles off Newport Beach where larval abundance was high (Figure 14, Table 1) and where samples from four tows each contained several emaciated larvae. The fact that these four samples showed a high proportion of emaciated larvae, while others from nearby tows showed only healthy larvae, indicates that there was a contagious or patchy distribution of such larvae off Newport Beach.

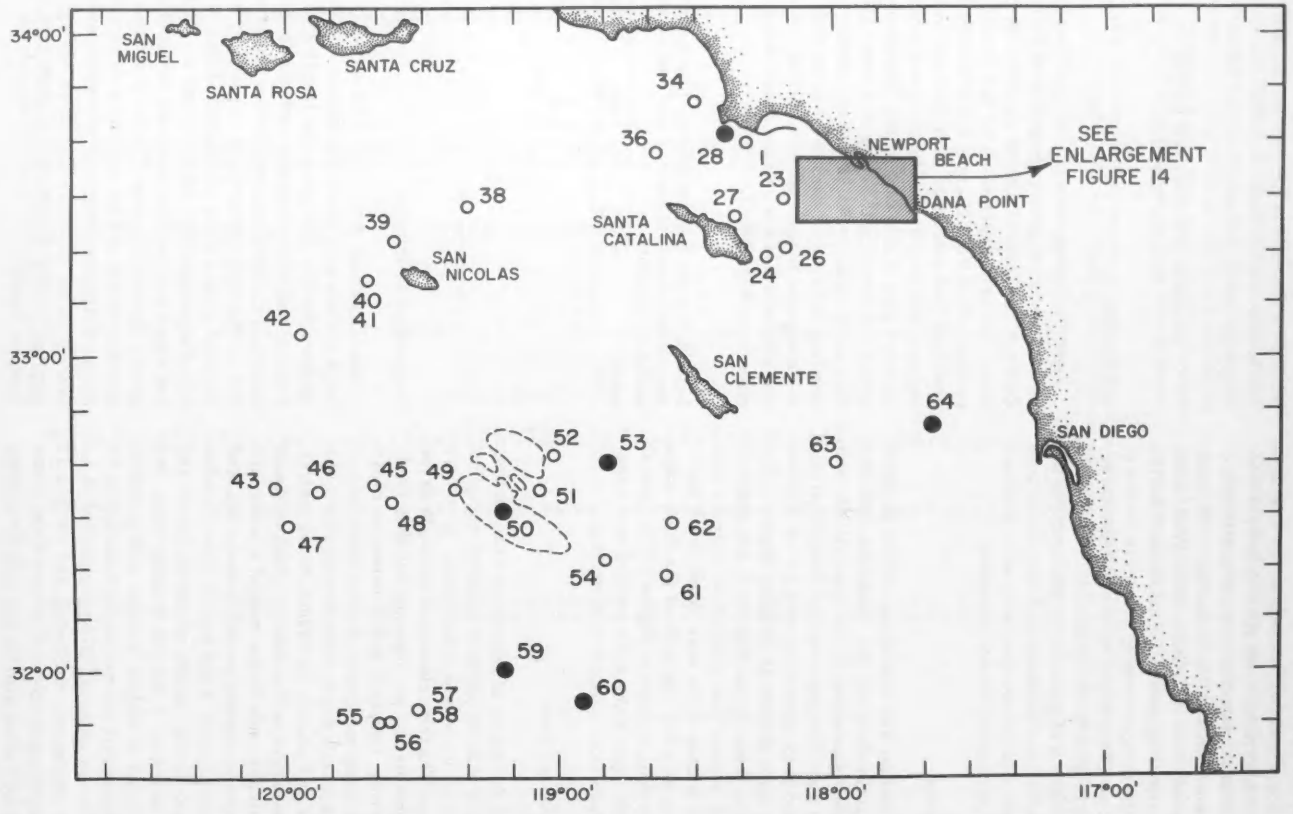


FIGURE 13.—The locations and sequence numbers of tows taken in March 1977 over the Southern California Bight, exclusive of the Newport Beach area. Open circles indicate tows from which all sectioned larvae were healthy, and dots indicate tows in which one of the sectioned larvae was emaciated. See Table 1 for data on tows.

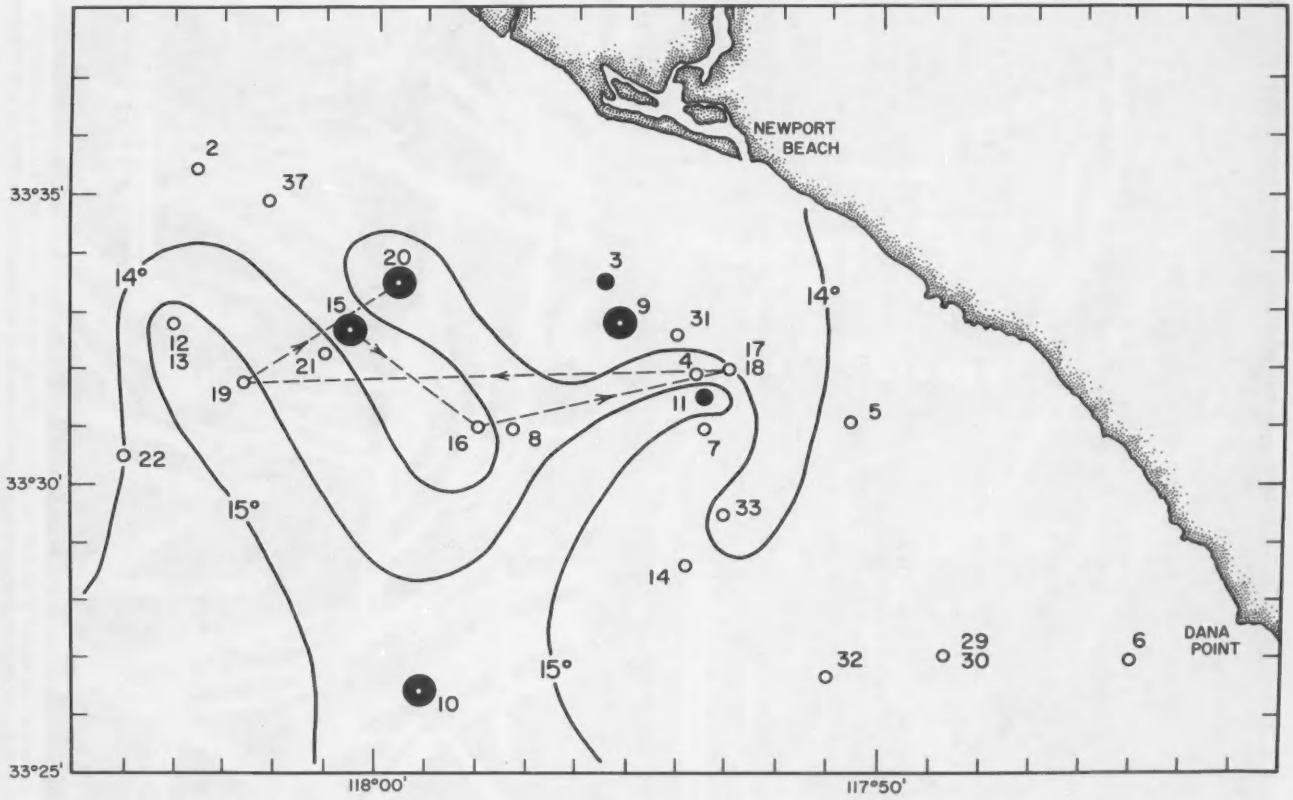


FIGURE 14.—The locations and sequence numbers of tows taken in the Newport Beach area, southern California. Open circles indicate tows from which all sectioned larvae were healthy; dots indicate tows from which one of the sectioned larvae was emaciated; larger dark circles with open centers indicate tows from which most of the sectioned larvae were emaciated; 1° C surface isotherms show that there was considerable temperature variation in the area; and dashed line is the cruise track for one 24-h period, and it indicates that the presence of emaciated larvae (tows 15 and 20) was persistent over at least this time span. See Table 1 for data on tows.

The impression of "patches" of larvae in poor condition indicated by the histological samples from the Newport Beach area was further strengthened by subsequent examination of the unsectioned larvae remaining from all net tows. Figure 15 shows a random portion of tow 23, which contained over 300 larvae and produced only healthy larvae in the histological sampling. The specimens are full-bodied with good symmetry and are straight, or at worst gently curved. Figure 16 shows a random portion of tow 9, which produced a high proportion of emaciated larvae in the histological sampling. Several of these larvae have angular body bends, trunks and digestive tracts that are lumpy and sinuous, and heads often misshapen with loose or missing eyes. They also appeared to be less intensely colored by the fixing solution than the others. When viewed in toto, this and the other three tow collections of larvae that produced histologically poor samples were readily distinguishable from all others.

The emaciated larvae consititute a percentage of the number of larvae examined, but the magnitude of this percentage depends on the portion of the total samples that are considered (Table 3). The four tows with a high incidence of emaciation, considered by themselves, indicate 60% emaciated larvae within local patches. This drops sharply to 12% when coverage is expanded to a few dozen tows in approximately 200 mi² off Newport Beach, and to 10% when an additional 10 tows, rather widely scattered over the San Pedro Channel area are included (inshore set). By comparison, the pooled offshore samples (offshore set) which represent perhaps 6,000 mi², indicate 5% emaciated, and samples pooled for the entire cruise show an intermediate value of 8% emaciated.

Day and night subsets of the inshore and offshore sets show differences in both the available population and the percentage of emaciated larvae. The lower daytime catches imply that the population was less available during this period, probably because much of it migrated below the 20 m depth of the tows during the day and probably also because larvae have some success in visually avoiding the net during the day. As a simple binomial function, the 15% emaciated larvae for the inshore night group is significantly higher

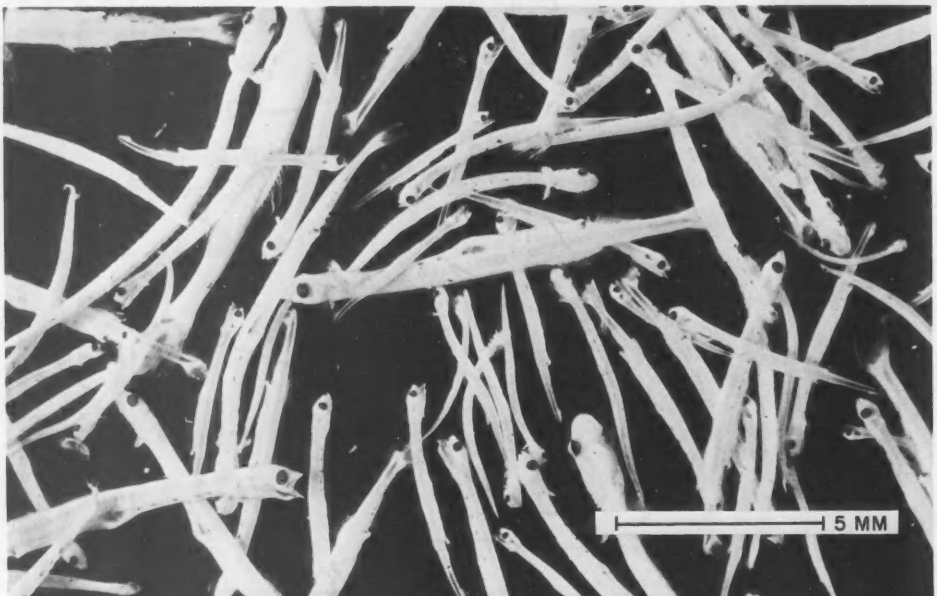


FIGURE 15.—A random portion of the northern anchovy larvae from tow 23, in which the larvae show generally good body form.

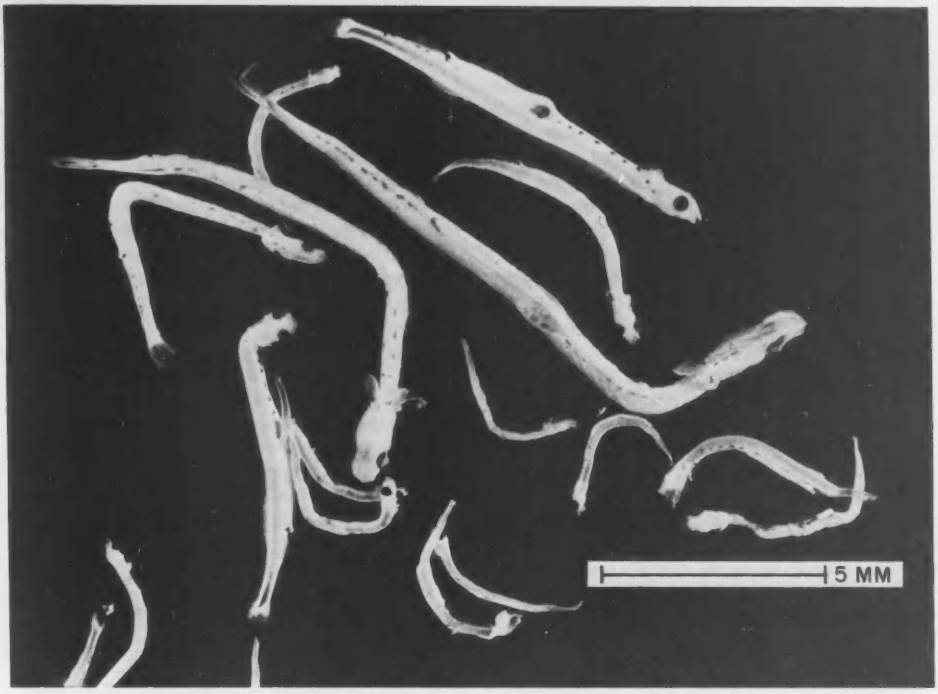


FIGURE 16.—A random portion of the northern anchovy larvae from tow 9, in which the larvae show generally irregular body form.

TABLE 3.—Percentage of emaciated northern anchovy larvae for different sample arrays.

Sample arrays	Number of tows	Larvae/ tow	Number of larvae examined	Number of larvae emaciated	Percent emaciated	95% confidence limits
Samples with high incidence of emaciation	4	37.5	30	18	60.0	±17.5
200 mi² coastal area includes above	27	77.1	165	20	12.1	± 5.0
Inshore set (tows 1-37):						
Day (0600-1800 h)	20	36.6	111	4	3.6	± 3.5
Night (1800-0600 h)	17	134.0	109	17	15.6	± 6.8
Pooled	37	81.3	220	21	9.6	± 3.9
Offshore set (tows 38-64):						
Day (0600-1800 h)	14	1.9	19	1	5.3	±10.0
Night (1800-0600 h)	13	11.2	79	4	5.1	± 4.8
Pooled	27	6.3	98	5	5.1	± 4.4
Total cruise pooled	64	50.0	318	26	8.2	± 3.0

than the other three subset percentages, but the obvious contagious nature of the distribution of these larvae casts doubt on the value of such tests. It is probably safer here to choose a lower percentage, such as the 8% for the entire cruise pooled, as representative, and assume that the observed subset differences are nothing more than sampling variation.

Surface Temperature

The tows with a high incidence of emaciated larvae were not associated with a given level of temperature, but it appears that they were located in an area of variable temperature (Figure 14). The 13° and 15° C tongues of water may have been basically persistent water masses, as Methot and

Kramer (1979) suggested, but the irregularity of the isotherms defining these tongues off Newport Beach implies local shifting of temperatures. Comparison of time as well as temperature differences along and adjacent to the cruise track for 20 March indicates, in fact, that notable temperature differences between closely located tows were probably more a matter of change over time than of static gradients between locations. Tows 15 and 20 are of particular interest because they both had a high incidence of emaciated larvae and were close together, but differed in temperature by 1.5° C. However, tow 20 was taken 24 h later than tow 15, and the thermograph record showed that the higher temperature applied to tow 15, as well as to the tow 19 and tow 20 positions, at the later time. Such short-term temperature shifts indicate that there was water mass instability or movement in the area.

Plankton Volume

Plankton volume averaged appreciably lower for the four tows with a high proportion of emaciated larvae than for either the inshore or the offshore set of tows (Table 4). The average number of larvae was also relatively low in these four tows, being about half the average for all tows off Newport Beach, or in the San Pedro Channel area (inshore set). Number of larvae and plankton volume, in fact, tend to be associated for the inshore set (Figure 17), and while the four tows with high incidence of emaciated larvae do not show the lowest values, they are among the tows with low values.

Plankton volume did not relate to temperature in the inshore area, but there were some interesting changes with time (Figure 18). From 17 March to midnight of 20 March all volumes were 11 ml or less. This includes the four tows with a high incidence of emaciated larvae, one of which (tow 20) was the last taken in this time period. Twenty-four hours later tow 21, the first tow with a markedly higher volume (21 ml), was taken at a nearby position (Figure 14). Three more tows of progressively higher volume were taken during night hours over the next few days, but there were also several tows with lower volumes (3-14 ml) taken during this period, some at night. This pattern indicates that there was a striking change in the plankton regime off Newport Beach starting on 21 March, with volume tending to be higher, especially at night, than it had been during the preced-

TABLE 4.—Mean plankton displacement volume (milliliters) for different sample arrays in the study of northern anchovy larvae off southern California.

Item	No. of tows	Larvae/ tow	Plankton Volume/ tow	Plankton SD
Samples with high incidence of emaciation	4	37.5	3.8	0.5
200 mi² coastal area includes above	27	77.1	8.3	9.3
Inshore set includes above	37	81.3	8.7	9.0
Offshore set	27	6.3	19.7	20.1
Total cruise	64	50.0	13.3	15.6

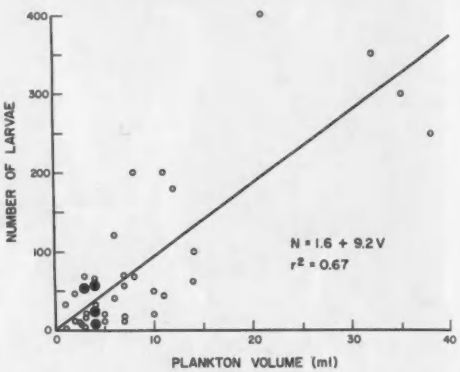


FIGURE 17.—The regression of number of anchovy larvae on displacement volume of plankton (larvae excluded) for the inshore tows, 1-37. The solid circles indicate the four tows with a high incidence of emaciated larvae.

FIGURE 18.—Displacement volume of plankton on date (March 1977) and hour of tow. Dots indicate the four tows with a high incidence of emaciated larvae. Dates are in bold type and located at midnight points on the hour scale.

ing few days, when the tows with a high incidence of emaciated larvae were taken.

DISCUSSION

The most significant result of this study is that northern anchovy larvae showing symptoms indicative of starvation were indeed found in the ocean and were thus identified on the basis of their individual appearance. The emaciated condition of these larvae is very similar to that induced in laboratory animals by total food deprivation (O'Connell 1976), which implies that circumstances of insufficient food were responsible for their occurrence in the ocean, especially where samples contained many such larvae, as off Newport Beach. Other causes are possible, and one of the most obvious is discharge from sewage outfalls in the area. However, the discharges are now diffused rapidly and in general appear to be harmless and perhaps even beneficial to nearby young and adult fish (Southern California Coastal Water Research Project[3]).

Zones of insufficient food might well have existed in the Newport Beach area at the time of the survey. The variations in both temperature and plankton volume, which were clearly dynamic in nature, indicate that there was appreciable water mass movement or instability, and such conditions can alter plankton abundance. Lasker (1975, in press) found, for example, that phytoplankton blooms believed to be advantageous for first feeding anchovy larvae were variously dissipated and suppressed as the water column became unstable in turbulent weather and sea conditions. In the present study the time sequence of plankton volume change off Newport Beach shows the possibility that water with relatively low plankton levels and "patches" of emaciated larvae was being replaced by water with greater plankton abundance, in which larvae were also more abundant and generally healthy.

Although the occurrence of zones of insufficient food is a reasonable hypothesis in regard to the "patches" of emaciated larvae off Newport Beach, it is not a plausible explanation for some of the other samples, where occasional emaciated individuals occurred among abundant healthy larvae. It can only be surmised that in any location, and despite generally good conditions, there will be some instances of starvation through detrimental combinations of genetic constitution, accident, and chance failure to capture food.

If circumstances of poor food availability are produced by water mass activity, as suggested above for the Newport Beach area, they are likely to be more or less transient phenomena, which raises the question of short-term susceptibility of northern anchovy larvae. Immediately after yolk absorption, northern anchovy larvae will survive only a day or two without food (Lasker et al. 1970), and they will show visible effects before dying (O'Connell 1976). Protein components are quickly affected because early postyolk-sac fish larvae have negligible lipid reserves (Ehrlich 1974), though such reserves obviously increase with growth and become a buffer against insufficient food (Love 1974). Even so, northern anchovy larvae of relatively large size, 35 mm SL, survived only 2 wk, on the average, after feeding was stopped, and during this period the average lipid content of living larvae was declining while mortality in the population was rising, with smaller individuals dying sooner than larger ones (Hunter 1976a). Since larvae examined in the present survey were appreciably smaller than the above, thus having lower lipid reserves, the signs of emaciation could have resulted from relatively few days of insufficient food.

Most of the larvae showing histological signs of emaciation in this study also showed signs of previous feeding, not by the presence of food residue, but rather by remnants of eosinophilic inclusion bodies in the hindgut mucosa cells. The starvation and previous feeding indications are not incompatible. Laboratory feeding studies have shown that growth, lipid content, and survival all decline quickly under limited or discontinued feeding (O'Connell and Raymond 1970; Hunter 1976a), and it is probable that histological signs of deterioration would also appear quickly, especially in early larval stages.

If, as proposed by Hjort (1914, 1926), the level of mortality suffered by the early feeding stages of fish populations is a decisive component of the prerecruitment mortality, some measure of that mortality should be a useful indicator of ultimate year class success. The proportion of larvae observed to be starving may be one such useful indicator: It is directly visible, and it may reflect a substantial part of total daily mortality. Zweifel and Smith (in press) have estimated average daily

[3]Southern California Coastal Water Research Project. 1978. The effects of the ocean disposal of municipal waste. Summary Report of the Commission of the Coastal Water Research Project, June 1978, 27 p. Filed at 1500 East Imperial Highway, El Segundo, CA 90245.

population abundance of larval anchovies by length and region for the 1967 through 1975 California Cooperative Oceanic Fisheries Investigations net tow data, and length dependent mortality rates were calculated from the abundance estimates. For larvae of 7.5 mm SL, which approximates the median length of those showing symptoms of starvation in the present study, the estimated average daily mortality rate in the San Pedro Channel area was 21%. If it is assumed that all larvae showing symptoms will die directly or indirectly from starvation, the observed 8% with symptoms in the March 1977 survey could indicate a net daily mortality from starvation of 8%, which is 40% of the average total daily mortality for this length group. If starvation tends to contribute this substantially to total mortality, variations in the proportion of larvae observed to be starving may relate reasonably well to the magnitude of ongoing total mortality and consequently to recruitment from the year class.

How well the proportion of starving larvae from a given sampling in 1 yr will predict the eventual recruitment of that year class will only be evident from correlation of the two variables for at least a few years. As for 1977, with a northern anchovy "starvation ratio" of 8%, there were indications that recruitment would be good. The winter and early spring were relatively mild, a condition conducive to development of high density patches of larval food organisms, particularly from dinoflagellate blooms (Lasker in press). Growth rate of northern anchovy larvae was also shown to be above average in the San Pedro Channel area for March 1977 (Methot and Kramer 1979). The above average growth rate may have been valid for much of the population developing in the region without applying to the patches of emaciated larvae, which were taken at different locations than the growth samples. Estimates from recent catch data indicate that the 1977 year class is of moderate size, as compared with the large 1976 and 1978 year classes and the small 1974 and 1975 year classes (J. S. Sunada[4]). Thus, to the extent that 8% starving larvae is a reliable estimate of that parameter for 1977 and to the extent that the parameter is associated with recruitment, both higher and lower occurrences of starving larvae are likely possibilities from future surveys.

[4]J. S. Sunada, Assistant Biologist, Marine Resources Region, California Department of Fish and Game, 350 Golden Shore, Long Beach, CA 90802, pers. commun. May 1979.

Reliability of the estimate of starving larvae is probably reasonably good for 1977 in that tows were most concentrated in a region of high abundance, but reliability in future sampling efforts could probably be improved by more diligent stratification in respect to population distribution. In addition to sampling at more than one point in time, an effective strategy might be to expand sampling in several areas that show high abundance, particularly of larvae under 10 mm SL, along a preplanned survey track. Expanding sampling in this way would likely result in a quantity of samples that would be formidable if analysis is entirely dependent on histological or physiological parameters. The distinctive appearance of the aggregated larvae from those few tows of the present survey that contained predominantly emaciated larvae, however, suggests that histological analysis can be greatly reduced.

Assuming that starvation of any consequence will occur in patches, a stereomicroscope scan of the total aggregation of larvae from each tow should suffice for the identification and enumeration of such patches, with histological processing reserved for selected verification. Undoubtedly some of the starving larvae that occur as scattered single cases would be missed under such a procedure, but this should have little effect on the overall estimate.

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I would like to acknowledge the very able assistance of Pedro Paloma, who sorted and measured all the samples and prepared all the slides.

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TRANSPORTATION OF CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, AND STEELHEAD, *SALMO GAIRDNERI*, SMOLTS IN THE COLUMBIA RIVER AND EFFECTS ON ADULT RETURNS

WESLEY J. EBEL[1]

ABSTRACT

Chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*, were captured at Little Goose Dam in the Snake River during their seaward migration and transported 400 km downstream to the lower Columbia River below Bonneville Dam. Their survival was increased from 1.1 to 15 times as compared with control fish which passed by seven mainstem low-level dams and reservoirs. Variations in survival were mainly dependent on species and environmental conditions in the river during the period fish were transported.

The homing ability of the adult fish was not significantly diminished; less than 0.2% of strays occurred among adult returns from groups transported. Transportation did not affect ocean age or size of returning adult steelhead, but ocean age of returning adult chinook salmon may have been affected. Steelhead returned to Little Goose Dam at a substantially higher rate (1.4-2.7%) than chinook salmon (0.1-0.8%) from groups transported. The timing of adult returns of both species to Little Goose Dam was not related to the time of capture and downstream release of smolts.

Salmonid populations of the Snake River and its Idaho tributaries have declined rapidly in recent years to the point that the very survival of some stocks is threatened. The total run (i.e., catch plus escapement) of chinook salmon, *Oncorhynchus tshawytscha*, attributable to the Snake River dropped from 120,000 adults in 1972 to 50,000 in 1974 (Raymond 1979). Similarly, the total run of steelhead, *Salmo gairdneri*, an anadromous form of rainbow trout, declined from 100,000 adults in 1972 to below 20,000 in 1974. The downward trend of the anadromous salmonid populations has been ascribed to losses of juvenile migrants at the series of eight dams (Figure 1) and associated reservoirs in the Snake and Columbia Rivers through which the smolts must pass on their way to the sea (Raymond 1979).

With the goal of protecting the migrants from the hazards of dams, a system for transporting smolts around the dams was investigated by the National Marine Fisheries Service. The juvenile migrants were collected from the Snake River at Little Goose Dam (the uppermost dam—Figure 1), transported around the entire series of dams, and released below Bonneville Dam (the lowermost dam) on the Columbia River. The effects of such transportation on the survival and catch of the fish and on the ability of the adults to "home" to their natal streams must be known if fishery agencies are to evaluate the transportation system as a practical means of protecting Snake River salmonid runs. The main objectives of the research at Little Goose Dam were: to determine the effect of transportation on homing and survival of juvenile chinook salmon and steelhead collected at Little Goose Dam and released at two locations downstream from Bonneville Dam and to compare these results with an earlier study done at Ice Harbor Dam (Ebel et al. 1973) where fish were

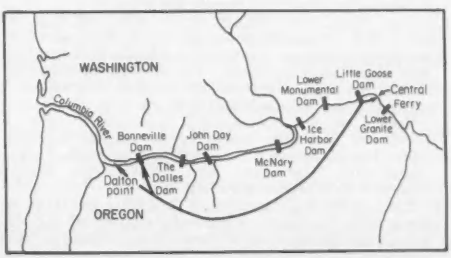

FIGURE 1.—Transportation routes and release location of experimental chinook salmon and steelhead collected and marked at Little Goose Dam, 1971-73.

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transported a shorter distance. Secondary objectives were: to determine any relation between timing of downstream juvenile migrants and timing of subsequent adult returns and to determine whether size and ocean age of adults (transported as smolts) were affected by the collection and transport process. The results of the experiments described in this report are also compared with the preliminary results of the current experiment at Lower Granite Dam.

BACKGROUND

The changes in abundance and the causes of changes in abundance of individual salmonid populations in the Columbia River drainage have been summarized by Chaney and Perry (1976). Raymond[2] analyzed the trends in abundance of Snake River runs in detail and clearly showed that the major causes of the decline of the Snake River stocks are due to the losses of juveniles during their seaward migration. These losses are caused by injury or death occuring when the fish attempt to pass the eight dams and reservoirs placed in their migratory path. These dams now inundate over 630 km of the migratory route. The main causes of the juvenile losses have been attributed to: passage through turbines (Bell et al.[3]; Long, Krcma, and Ossiander[4]; Long, Ossiander, Ruehle, and Mathews[5]); supersaturation of river water with atmospheric gas (Ebel and Raymond 1976); delay in migration (Raymond 1968, 1969); and increased predation (Chaney and Perry 1976).

The National Marine Fisheries Service (NMFS) has been conducting transportation experiments since 1965 in an attempt to find ways of reducing these losses. The first study where natually migrating juveniles were collected and transported was conducted by Ebel et al. (1973). This study showed that the homing ability of adult spring and summer chinook salmon and steelhead captured during their seaward migration as juveniles and then transported downstream (from Ice Harbor Dam to below Bonneville Dam) was not diminished. Data based on returning adults indicated that survival rate of adult fish that had been transported as juveniles increased 1.5-3 times the survival rate of those not transported, depending on environmental conditions in the river during the time of transport. Studies conducted prior to this study with hatchery stocks of salmonids showed that the majority of the adult fish that had been transported as juveniles returned to the release site, not to the parent location (Snyder 1928; Ellis and Noble 1960). Obviously, juvenile salmonids captured during their seaward migration and then transported differed in their responses from fish transported directly from hatcheries. The wild and hatchery stocks captured in the experiment conducted by Ebel et al. (1973) were smolting and had traversed several hundred kilometers before capture. These may be the main factors causing the different response (homing ability was not diminished) obtained in the experiment done in 1973.

Previous experiments (Hasler and Wisby 1951; Groves et al. 1968; Scholz et al. 1973) on mechanisms used by fish for homing indicated that the experience prior to and during the time that a juvenile salmon migrates is important in enabling the fish to receive visual and olfactory cues necessary for homing as an adult.

Only a portion of the migration route was eliminated by transporting the fish from Ice Harbor Dam to The Dalles and Bonneville Dams. Elimination of this portion of the migratory route apparently did not seriously affect the ability of either the chinook salmon or steelhead to home. However, the length of the migration route or amount of homing cues that can be eliminated and still achieve satisfactory homing is unknown.

The success of the experiment by Ebel et al. (1973) at Ice Harbor Dam encouraged the NMFS to begin a similar experiment at Little Goose Dam in 1971. As this dam is approximately 130 km upstream from Ice Harbor Dam, an additional 130

[2]Raymond, H. L. 1975. Snake River runs of salmon and steelhead trout: trends in abundance of adults and downstream survival of juveniles. Unpubl. manuscr., 11 p. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[3]Bell, M. C., A. C. DeLacy, G. J. Paulik, and R. A. Winnor. 1967. A compendium on the success of passage of small fish through turbines. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112. (Contract DA-35-026-CIVENG-66-16, Report to U.S. Army Corps of Engineers, Portland, Oreg.)

[4]Long, C. W., R. F. Krcma, and F. J. Ossiander. 1968. Research on fingerling mortality in Kaplan turbines—1968. Unpubl. manuscr., 7 p. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[5]Long, C. W., F. J. Ossiander, T. E. Ruehle, and G. M. Mathews. 1975. Final report on survival of coho salmon fingerlings passing through operating turbines with and without perforated bulkheads and of steelhead trout fingerlings passing through spillways with and without a flow deflector. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112. (Contract DACW68-74C-0113, Report to U.S. Army Corps of Engineers, Portland, Oreg.)

km of the migratory route would be eliminated, and the fish would be intercepted during their juvenile migratory life stage about 2-3 wk earlier than they were at Ice Harbor Dam. The results achieved at this site could be quite different from those obtained at Ice Harbor Dam. To facilitate the collection of fish, an orifice bypass system, juvenile fish diversion screens, and raceways for collection of juvenile fish were built into Little Goose Dam during its construction. This system provided substantial numbers of fish for the experiment, but there was the possibility that these fish might be injured or stressed during the diversion and collection process.

TABLE 1.—Number of transported and nontransported (control) juvenile chinook salmon and steelhead that were marked and released from Little Goose Dam, 1971-73.

Species and release year	Control fish	Transported fish[1]	
		Dalton Point	Bonneville Dam
	No. released[2]	No. released[2]	No. released[2]
Chinook salmon:			
1971	20,673	30,637	35,252
1972	32,836	51,499	54,906
1973	88,170	57,758	83,606
Steelhead:			
1971	33,243	35,967	44,939
1972	32,488	22,831	27,326
1973	42,461	26,650	36,802

[1]Transported fish were released in the Columbia River at two sites downstream from Bonneville Dam: 2 km downstream on the Washington (side referred to in the table as Bonneville Dam) and 17 km downstream on the Oregon side at Dalton Point.
[2]Release totals adjusted for initial tag loss.

METHODS

Experimental Design

During the downstream migrations in 1971, 1972, and 1973 juvenile chinook salmon and steelhead were randomly selected from the raceways at Little Goose Dam and divided into three groups—one control and two transported groups. The adipose fin was removed from all experimental fish and each group was selectively marked with a thermal brand and magnetized wire tags. Thermal brands were changed every 5 d among all treatment groups except for the first 10-d marking period. During this period, marking continued for 10 d before a change was made. Codes for magnetized wire tags were changed yearly for each treatment group. The control group was released at Central Ferry, about 10 km upstream from Little Goose Dam; the transported groups were hauled in tank trucks to two locations downstream from Bonneville Dam (Figure 1). One release site was at Dalton Point, 17 km downstream from Bonneville on the Oregon side of the river; the other was at the Washington State boat launching site, about 2 km downstream from Bonneville Dam. Each year the goal was to mark at least 50,000 chinook salmon and 25,000 steelhead for each group. This goal was exceeded every year (Table 1) except for all groups of chinook salmon in 1971 and the control group of chinook salmon in 1972.

Collection and Marking of Fish and Fish Hauling Procedures

Juvenile chinook salmon and steelhead were collected at Little Goose Dam, using a fingerling collection and bypass system (Smith and Farr 1974). The system consisted of: 1) screens in the turbine intakes which diverted fish into the gatewells of each turbine intake; 2) a gatewell orifice and piping system which transported fish from the gatewells to a grader and counter; and 3) a fish grader and counter which sorted fish by size and electronically counted fish entering five raceways. When desired, fish could be diverted directly to the river—thus bypassing the grader, counter, and raceways.

Fingerling chinook salmon and steelhead were pumped with a 5-in Paco model fish pump into the marking building where they were anesthetized and sorted. Previously marked fish were returned to the river in the tailrace of the turbine discharge. Samples of at least 100 chinook salmon and steelhead were examined each day for percentage descaling to provide an index of fish condition. Any fish with >10% of the scales missing was considered descaled. Each of the remaining fish was cold-branded with liquid nitrogen (Park and Ebel 1974), had the adipose fin excised, and had a magnetic wire tag (Jefferts et al. 1963) inserted in the snout. Before passing into a transport truck, the fish went through a magnetic field and detection coil; an untagged fish was automatically rejected and returned to the marker for retagging. Initial tag loss was measured by examining samples of juveniles 48-72 h after tagging; subsequent tag loss was determined by examining returns of adult control and test fish at Rapid River Hatchery near Riggins, Idaho, and Dworshak National Fish Hatchery at Ahsahka, Idaho. A branded fish with an adipose fin clip that did not also have a coded

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

wire tag was considered a fish that had lost its tag after marking. Steelhead and chinook salmon were kept in separate compartments in the tank truck whenever both species were hauled simultaneously. All fish were transported in a truck of 18,900 l (5,000 gal) capacity (Smith and Ebel 1973) that was equipped with aeration, refrigeration, and filtration systems. Load densities were governed by the size of the daily catch and were usually <0.12 kg/l (1 lb/gal) except during periods when unmarked fish were hauled. Maximum load density was kept <0.18 kg/l (1.5 lbs/gal) of water.

Water chemistry measurements were taken from the truck at the time of release for every load transported. Concentrations of ammonia, nitrogen, dissolved oxygen, carbon dioxide, pH, and total alkalinity were recorded for possible correlations with delayed mortality information. All releases were made at dusk. Records of mortality were kept during marking and at time of release; a sample of 50-100 fish was taken from each transported load and held for 48 h at Bonneville Dam to provide an indication of delayed mortality. This procedure was repeated during downstream migrations in 1971, 1972, and 1973.

Evaluation of Returning Adults

The effect of transportation on the survival and homing of adult fish was evaluated by comparing returns of transported and nontransported fish to the sport, commercial, and Indian fisheries in the lower Columbia River; to Little Goose Dam on the lower Snake River; to Rapid River Hatchery, Pahsimeroi Hatchery near Salmon, Idaho, and Dworshak Hatchery; and to the spawning grounds throughout the Snake River drainage.

All adult fish migrating upstream at Little Goose Dam must ascend one ladder located on the south side of the dam. An adult tag detection and fish separating device that intercepted tagged salmon and steelhead and diverted them into a holding pen was installed in this ladder in 1972 (Ebel 1974). Tagged fish from our study were readily identified by the missing adipose fin. All fish were anesthetized and further examined for brands. If the brand was recognizable, the origin of the fish could be determined without having to extract the magnetic tag from the snout.

Fish with recognizable brands were then weighed and measured, dart-tagged or jaw-tagged (Slatick 1976), and released to provide further information in the event of recapture upstream and to identify fish that fell back over the dam and ascended the ladder a second time. If a fish was known to be tagged but had a brand that was indistinguishable, it was held until maturity in holding tanks at the dam and artificially spawned. The tag was then extracted after spawning, and the test or control group was determined from the color code. Data obtained from these fish were combined with those obtained from reading brands.

The Columbia River gillnet fishery below Bonneville Dam, the Indian fishery above the dam, and the sport fishery (primarily below the dam) provided samples of chinook salmon throughout the spring run. The samples yielded information concerning the returns to the lower river of marked fish originating primarily in Idaho. Closure of the summer fishery on chinook salmon during all 3 yr and the spring fishery in 1974 and 1975 prevented sampling of this segment of the run in the lower river. The sport and commercial fisheries of the lower Columbia River and the sport fishery above Little Goose Dam provided samples of steelhead.

Surveys of spawning grounds were conducted with the cooperation of the Washington Department of Fisheries, Fish Commission of Oregon, and the Idaho Department of Fish and Game. Most of the surveys were in the Snake River drainage of Idaho, but hatcheries and spawning grounds of spring and summer chinook salmon in the upper Columbia River were also checked for strays.

The G statistic, Student's *t*-test, and analysis of variance were used for analysis of most return data.

RESULTS

Factors Influencing Assessment of Data

Tag loss, tag detector efficiency, transport mortality, and delayed mortality were factors that influenced the assessment of the experimental data. Comparisons of tests and control releases could be biased if a differential effect among any of these factors occurred between test and control releases and was not considered in the analysis. For example, if tag loss was greater in control releases than in test releases, percentage return would be biased in favor of the test release if the data were not adjusted for this loss.

During the 3 yr of this study, average annual initial tag loss ranged from 0.45% in 1973 to 10.4%

in 1972; average tag loss for the 3 yr of marking was 3.7%. Release totals were adjusted for initial tag loss. Additional tag loss (occurring after initial tag loss), based on examination of 884 marked adult steelhead at Dworshak National Fish Hatchery and 154 marked adult chinook salmon at Rapid River Fish Hatchery, was nill (<0.1%) and did not affect data analysis.

About 4-8% of the juvenile chinook salmon and 4-10% (Park et al.[7]) of the juvenile steelhead released as controls were recaptured and released at Little Goose Dam. No attempt was made to adjust the data for a small bias that might have occurred from this procedure. It was assumed that survival of this portion of the controls that were handled and released after passing through the collection system was the same or greater than survival of the majority of the control fish that had to pass either through the turbines or over the spillway.

The primary recovery site for evaluation of tag returns was at Little Goose Dam where an automatic tag detector and fish trap were installed (Ebel 1974). The efficiency of the detector and trap was based on a comparison of known recovery of fish with magnetized wire tags at Little Goose Dam and subsequent recovery of these and other marked fish at Rapid River and Dworshak Hatcheries. For example, 54 fish were identified at Rapid River Hatchery in 1975 from treatment groups that had passed Little Goose Dam. Of these, 50 had jaw tags indicating they had been captured and identified at Little Goose Dam; 4 did not have jaw tags indicating these fish had passed the dam without being trapped or identified. The trap efficiency for chinook salmon in 1975 was therefore 50/54 or 0.92. Thus, a factor of 1.08 was used to expand recoveries of .2- and .3-age[8] chinook salmon captured and identified at Little Goose Dam in 1975 from experimental releases in 1972 and 1973. Similar calculations were made for each year of recovery of chinook salmon during 1972-76 in computing estimated percentage return for a particular treatment group. The same procedure was used to estimate trap efficiency for steelhead with data obtained from recoveries at Dworshak Hatchery. The efficiency of recovery varied among years from 43 to 90% during the spring and summer when tagged chinook salmon were recovered. One source of variation was due to periodic shutdowns of the detector and trap for special studies of passage of adult fish. The efficiency remained constant (72%) during the fall of each year when most adult steelhead were recovered. An examination of the timing of test and control fish returning to Little Goose Dam indicated there was no significant difference. Thus, variations in efficiency did not affect comparisons of recoveries of test and control fish because all experimental groups passed the detector throughout the recovery period, and both test and control groups were subjected to the same variations in recovery efficiency. Total estimates of adult returns were adjusted for detector efficiency for a given period of recovery.

The use of the above method of estimating total percentage return for treatment groups assumes: loss of jaw tags from fish identified at Little Goose Dam was nil and jaw-tagged fish survived at the same rate as fish not jaw tagged. The first assumption is valid, I believe, because examination of several hundred fish at both Dworshak and Rapid River Hatcheries each year of recovery did not reveal any evidence of lost tags. Data from recent radio tracking studies (see Monan and Liscom[9]) suggest that the second assumption is also valid. In these studies, adult chinook salmon were obtained from the fish ladder with a similar trap and handled in an identical manner before tagging, and mortality of tagged fish was nil.

Transport mortality was defined as the mortality which occurred as a result of handling, marking, and hauling; delayed mortality was considered mortality that occurred in samples held at Bonneville Dam immediately after hauling. Transport mortality of both species was <1% of the total number of smolts handled (Table 2). Delayed mortality (Table 3) was considerably more, ranging from 10 to 22% for chinook salmon and 1.0 to 4.5% for steelhead. Transport and delayed mortality obviously reduced the total number of

[7]Park, D. L., J. R. Smith, E. Slatick, G. Matthews, L. R. Basham, and G. A. Swan. 1978. Evaluation of fish protective facilities at Little Goose and Lower Granite Dams and review of mass transportation activities, 1977. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112. (Contract DACW68-77-0043, Report to U.S. Army Corps of Engineers, Portland, Oreg.)

[8]Age designations follow the formulas of Koo (1962). The number of winters at sea is shown by an Arabic numeral preceded by a dot.

[9]Monan, G. E., and K. L. Liscom. 1974. Radio-tracking of spring chinook salmon to determine effect of spillway deflectors on passage at Lower Monumental Dam, 1973. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112. (Contract DACW57-73-F-0534, Final Report to U.S. Army Corps of Engineers, Portland, Oreg.)

TABLE 2.—Mean mortality of juvenile chinook salmon and steelhead during transport from Little Goose Dam to release locations downstream from Bonneville Dam, 1971-73.

	Percentage mortality		
Species	1971	1972	1973
Chinook salmon	0.87	0.57	0.70
Steelhead	0.16	0.51	0.51

TABLE 3.—Mean delayed mortality of samples of juvenile chinook salmon and steelhead taken from marked groups transported from Little Goose to below Bonneville Dam. Fish were held from 48 to 72 h after transport.

	Percentage mortality		
Species	1971	1972	1973
Chinook salmon	22.8	10.0	17.2
Steelhead	1.0	1.4	4.5

transported smolts released and correspondingly reduced adult returns from transported groups. Control groups may have been less affected because of the shorter transport time (1 h vs. 6 h). However, the assessment of benefits or losses obtained from transport of salmonid smolts must include this mortality. Release totals were therefore not adjusted for either transport or delayed mortality. It was noted that over 90% of the dead fish in the delayed mortality group had obvious signs of descaling or injury.

Measurements of descaling (fish with >10% of the body area descaled) of chinook salmon smolts that were recorded during the marking process varied from 0 to as high as 50% of the individuals observed. The average annual descaling rate was 16.6% in 1972 and 19.6% in 1973. Incomplete records of descaling measurements made it impossible to determine the average rate of 1971. Descaling of steelhead was substantially less than descaling of chinook salmon; the overall average for 1972 and 1973 was <1%. It was determined from other studies being conducted that most of the descaling was caused by experimental diversion screens being tested in the turbine intakes (Ebel et al.[10]).

There was a relation between descaling rate and delayed mortality. Steelhead were less descaled than chinook salmon and had much less delayed mortality than chinook salmon. It appears that if the injury that occurred during diversion and handling could be eliminated, survival of transported chinook salmon could be substantially improved.

Returns of Adult Experimental Fish to Little Goose Dam

A comparison of ratios of transport and control percentage returns of adults to Little Goose Dam from releases of chinook salmon and steelhead for the 3 yr of this study (Figure 2) indicated that survival of both species was substantially increased in 1973 by transporting the fish to the Dalton Point and Bonneville Dam release sites.

The percentage increase in survival varied from year to year and, I believe, was dependent primar-

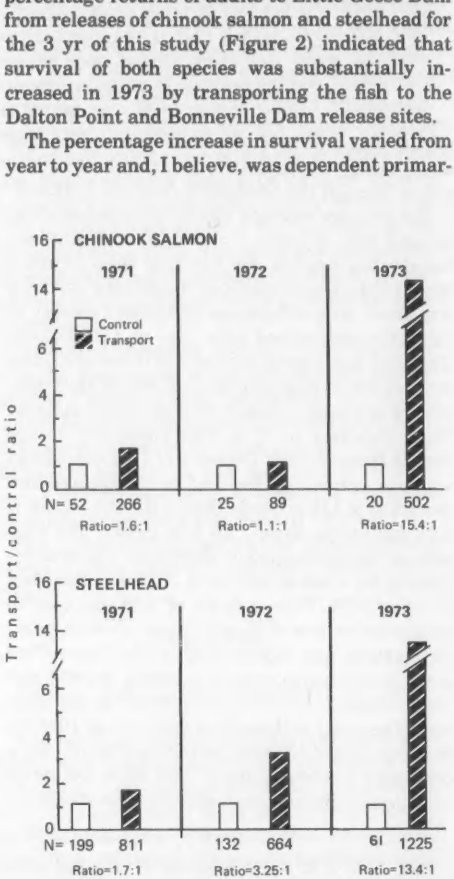

FIGURE 2.—Comparison of ratios of adult percentage return to Little Goose Dam from control and transported juvenile chinook salmon and steelhead. (Returns from Dalton Point and Bonneville Dam releases combined.) Percentage return of controls was set at unity for each year and species; the increase (transport percentage return ÷ control percentage return) is shown by darkened bar.

[10]Ebel, W. J., R. F. Krcma, and H. L. Raymond. 1973. Evaluation of fish protective facilities at Little Goose Dam and review of other studies relating to protection of other salmonids in the Columbia and Snake River, 1973. 62 p. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112. (Contract DACW68-71-0093, Progress Rep. to U.S. Army Corps of Engineers, Portland, Oreg.)

ily on river conditions. During years when survival of natural migrants (hatchery and wild stocks migrating naturally) was low, there was correspondingly low survival of control releases and greatest benefit from transportation. For example, in 1973, natural migrant survival estimates (Raymond 1979, see footnote 2) indicated an all-time low survival rate for both juvenile chinook salmon and steelhead migrants; in contrast, transport-control ratios were highest—15.4:1 for chinook salmon and 13.4:1 for steelhead (Figure 2). Raymond (1979) compared survival estimates of control releases from this study and other earlier studies (Ebel et al. 1973; Slatick et al. 1975) with survival estimates of naturally migrating smolts and found a high correlation ($r = 0.95$ for chinook salmon; 0.92 for steelhead) between survival of controls from transportation studies and his estimates of survival of natural migrants for the years 1968 to 1975. These data indicated there were close relationships between survival of releases of control fish marked for the transportation studies and hatchery and wild stocks migrating naturally. Raymond also correlated low survival with adverse river conditions; thus benefits from transportation would be highest when river conditions are the most adverse.

Statistical analysis of the return percentages (Table 4) was done by analysis of variance. A test of normality (Shapiro and Wilk 1965) of the percentage return data showed that the data were normally distributed ($P<0.05$); thus, transformation of percentage figures was not necessary. Analysis of variance of the return percentages indicated that the differences between "treatments" (test and control releases) were significant at the 1% level (Table 5). Interactions of the treatment × species were significant at the 5% level, indicating that the effects of treatment varied between chinook salmon and steelhead. For example, the mean transport/control ratio for returning chinook salmon in 1972 was 1.1:1, whereas the mean ratio for steelhead was 3.25:1. An analysis of the test of treatment effects—to compare the two downstream releases (both transported) and the control vs. the transported groups (Table 5)—clearly showed that there were no differences between recoveries from the Dalton Point and Bonneville Dam release sites and that the differences shown between test and control groups (Figure 2) were highly significant ($P<0.01$). Since interactions of the treatment × species were significant ($P<0.05$), I also analyzed the chinook salmon and steelhead percentages separately (Table 6). These analyses confirmed that differences shown between test and control groups were significant ($P<0.05$) for both steelhead and chinook salmon and that there were no differences between re-

TABLE 4.—Releases and recaptures of experimental fish.

Species, release site, and year	Number released	Ocean age[1] (no.) .1	.2	.3	Total	Adult returns (%) Observed	Estimated[2]	Transport/control ratio[3]
Chinook salmon[4]:								
Control:								
1971	20,673	5	28	19	52	0.252	0.470	
1972	32,836	4	12	9	25	0.076	0.106	
1973	88,170	2	11	7	20	0.023	0.026	
Transport:								
Dalton Point:								
1971	30,637	9	70	40	119	0.388	0.760	1.6:1
1972	51,499	4	20	20	44	0.085	0.114	1.1:1
1973	57,758	35	130	76	241	0.417	0.730	28.1:1
Bonneville Dam:								
1971	35,252	11	83	53	147	0.417	0.785	1.7:1
1972	54,906	5	28	12	45	0.082	0.110	1.0:1
1973	83,606	34	142	85	261	0.312	0.438	12.2:1
Steelhead:								
Control:								
1971	33,243	75	121	3	199	0.599	0.833	
1972	32,488	75	57	—	132	0.406	0.564	
1973	42,461	20	41	—	61	0.144	0.199	
Transport:								
Dalton Point:								
1971	35,967	124	237	6	367	1.020	1.418	1.7:1
1972	22,831	187	130	1	318	1.393	1.936	3.6:1
1973	26,650	276	276	5	517	1.940	2.698	13.5:1
Bonneville Dam:								
1971	44,939	166	287	11	464	1.033	1.436	1.7:1
1972	27,326	202	139	5	346	1.266	1.750	3.1:1
1973	36,802	352	353	3	708	1.924	2.673	13.4:1

[1]Age designation follows the formulas of Koo (1962). The number of years at sea is shown by an Arabic numeral preceded by a dot.
[2]Return percentage adjusted according to tag detector and trap efficiency.
[3]Transport/control ratios determined by dividing estimated percentage return of controls into estimated return of transported fish.
[4]Adult returns of spring and summer chinook salmon combined.

TABLE 5.—Analysis of variance of comparative percentage returns of adult chinook salmon and steelhead to Little Goose Dam for transported and nontransported (control) juveniles, 1971-73.

Source	df	SS	MS	Pooled residual (F)	Residual (F)
Treatments (test and control returns)	2	3.053	1.526253	8.924**	12.717**
Years (1971-73)	2	0.398	0.198794	1.162	1.657
Species (chinook and steelhead)	1	5.520	5.520057	32.276**	46.005**
Treatment × years	4	0.890077	0.223	—	1.858
Treatment × species	2	1.356179	0.678	3.965	5.650*
Years × species	2	0.698503	0.349	2.042	2.908
Residual	4	0.478141	0.120	—	—
Pooled residual	8	1.368218	0.171	—	—
Total	17	13.762118			
Partition of treatment SS (above), comparing adult chinook salmon and steelhead returns for control vs. transport and Dalton Point vs. Bonneville Dam.					
Control vs. transport	1	3.035	3.035	17.743**	
Bonneville vs. Dalton Point	1	0.018	0.018	0.105	

*$P<0.05$; **$P<0.01$.

TABLE 6.—Analysis of variance of comparative percentage returns of adult chinook salmon and steelhead to Little Goose Dam for transported and nontransported (control) juveniles, 1971-73 (returns analyzed by species).

Chinook salmon return data Source	df	SS	MS	F
Treatments (test and control returns)	2	0.179	0.089	2.70
Years (1971-73)	2	0.473	0.237	7.14*
Error	4	0.132	0.033	
Total	8	0.7849		
Partition of treatment sum of squares (above) comparing adult chinook salmon returns for control vs. transport and Dalton Point vs. Bonneville Dam.				
Control vs. transport	1	1.604	1.604	48.45**
Bonneville vs. Dalton Point	1	0.014	0.014	0.4342NS
Steelhead return data **Source**	**df**	**SS**	**MS**	**F**
Treatments (test and control returns)	2	4.230	2.115	6.845
Years (1971-73)	2	0.623	0.311	1.006
Error	4	1.236	0.309	
Total	8	6.089		
Partition of treatment sum of squares (above) comparing adult steelhead returns for control vs. transport and Dalton Point vs.Bonneville Dam.				
Control vs. transport	1	4.223	4.223	13.667*
Bonneville vs. Dalton Point	1	0.062	0.062	0.020NS

* = $P<0.05$; ** = $P<0.01$; NS = nonsignificance.

coveries from the Dalton Point and Bonneville Dam release sites for either chinook salmon or steelhead.

Percentage Adult Returns of Transported Releases

Analysis of the transport/control ratio provides the best insight as to the possible benefits from the transportation system, but total percentage return obtained from the groups transported must also be examined to accurately assess the effectiveness of the system as it operated. If both transport and control groups were excessively stressed during the diversion, collection, marking, and transport operations, then percentage returns would have been abnormally low even though transport/control ratios were favorable. I, therefore, compared percentage returns of the transport groups with percentage returns of production releases achieved at Dworshak and Rapid River Hatcheries and with estimated percentage returns of steelhead and chinook salmon to Little Goose Dam.

Returns from production releases of juvenile steelhead at Dworshak Hatchery (Olson[11]) were 0.25% in 1971, 0.20% in 1972, and 0.052% in 1973. Corresponding estimated percentage returns of steelhead from those transported from Little Goose Dam in 1971, 1972, and 1973 (returns from Dalton Point and Bonneville Dam releases combined) were 1.4, 1.8, and 2.7%, respectively. Although the sport fishery for steelhead above Little Goose Dam in 1973 would have reduced the percentage returns to Dworshak for releases in 1971, the estimated catch of 2,459 (Petit[12]) when added to the total hatchery returns, resulted in a return percentage of <0.50 for the 1971 release. The sport fishery was closed from 1974 to 1976; thus returns from releases in 1972 and 1973 at Dworshak Hatchery were not affected.

I also compared percentage adult returns of steelhead with the estimated percentage adult returns from populations of natural migrants passing Little Goose Dam in 1971, 1972, and 1973 by Raymond (1979, see footnote 2). His estimates of percentage returns were based on counts of adults passing the dam and estimates of populations of smolts (both hatchery and wild) passing Little Goose Dam for a given year. His estimates of percentage adult returns of steelhead to Little Goose

[11]Wayne Olson, Hatchery Manager, Dworshak National Fish Hatchery, Ahsahka, Idaho, pers commun. 1973-76.

[12]Steven Petit, Senior Fisheries Research Biologist, Idaho Fish and Game Dep., Lewiston, Idaho, pers. commun. June 1974.

Dam for 1971, 1972, and 1973 were 0.8, 0.4, and 0.2%, respectively. These estimates did not include fish that were transported. A substantial increase in survival of transported steelhead is indicated by both analysis of test/control ratios and comparisons of percentage returns of adults from transported groups with percentage returns of adults to Dworshak Hatchery and Little Goose Dam.

Percentage returns from production releases of juvenile chinook salmon to Rapid River Hatchery (Parrish[13]) in 1971, 1972, and 1973 were 0.59, 0.12, and 0.15%, respectively. The corresponding percentage returns from juvenile chinook salmon transported from Little Goose Dam were 0.77, 0.11, and 0.52%, respectively. Estimated adult returns (Raymond 1979, see footnote 2) of the mixture of wild and hatchery populations of juvenile chinook salmon passing Little Goose Dam in 1971, 1972, and 1973 were 1.3, 0.6, and 0.4%, respectively. While some benefit can be shown when percentage return data from transported groups are compared with only the Rapid River Hatchery returns for 1971 and 1973, only those transported in 1973 showed a benefit when returns were compared with estimated percentage returns of adults from mixed wild and hatchery smolts passing Little Goose Dam.

When the combined returns of spring and summer chinook salmon were divided into seasonal races (Table 7) and compared for the 3 yr of this study, the benefits or losses from transportation were defined by time. Transport/control ratios indicated that spring chinook salmon received greater benefit from transportation in 1971 and 1973 than summer chinook salmon. Summer chinook salmon appeared to receive more benefit than spring chinook salmon in 1972, but returns from all chinook salmon releases were low in 1972.

Several factors could be responsible for the differential in transport/control ratios between spring and summer chinook salmon among the years. Probably the most important factor was the timing of seaward migration of the two races of salmon. The race migrating downstream during the most favorable river conditions would receive the least benefit from transport in any particular year.

[13]Evan Parrish, Hatchery Manager, Idaho Fish and Game Dep., Rapid River Hatchery, Riggins, Idaho, pers commun. 1973-76.

Timing of Adult Returns of Chinook Salmon

Analysis of data on timing of adult returns in comparison with timing of the juvenile seaward migration (Table 8) indicated that the timing of adult returns of chinook salmon to Little Goose Dam was independent of timing of juvenile seaward migration ($G = 0.518, 0.516$, and 0.293: $df = 1, P<0.05$ for 1971, 1972, and 1973, respectively). This is in contrast to what Ebel et al. (1973) found in adult chinook salmon returning from groups marked at Ice Harbor Dam in 1968. In this study most of the chinook salmon marked early in the spring migration returned early as spring chinook salmon, and most of those marked late returned later as summer chinook salmon. Perhaps intercepting the fish 130 km farther upstream eliminated the relation indicated from the earlier study. It is also possible that races of chinook salmon that exhibited this behavior in 1968 were absent or very low in numbers during 1971-73.

TABLE 8.—G-statistic test of relationship between timing of adult returns of chinook salmon to timing of juvenile seaward migration at Little Goose Dam, 1971-73.

Juvenile migration		Adult returns				
Year	Period[1]	Spring[2] (no.)	Summer[3] (no.)	Total (no.)	G	Significance[4]
1971	Early	73	25	98		
	Late	120	33	153		
	Total	193	58	251	0.518	NS
1972	Early	22	23	45		
	Late	14	10	24		
	Total	36	33	69	0.516	NS
1973	Early	149	86	235		
	Late	122	63	185		
	Total	271	149	420	0.293	NS

[1]Early = marked as juveniles from beginning of migration to 5 May. Late = marked as juveniles after 5 May.
[2]Prior to 15 June.
[3]After 14 June.
[4]$P>0.05$, $df = 1$; NS (nonsignificance) indicates timing of adult returns is independent of timing of seaward migration.

TABLE 7.—A comparison of adult returns to Little Goose Dam of transported and nontransported (control) spring and summer chinook salmon smolts, 1971-73. Percentage values indicate adult returns from transported group.

Seasonal race of chinook	1971					1972					1973				
	Control		Transport		Ratio transport/ control	Control		Transport		Ratio transport/ control	Control		Transport		Ratio transport/ control
	No.	%	No.	%		No.	%	No.	%		No.	%	No.	%	
Spring	37	0.179	200	0.303	1.70:1	18	0.055	65	0.061	1.1:1	10	0.011	329	0.232	21.2:1
Summer	15	0.073	66	0.100	1.37:1	5	0.009	24	0.022	2.4:1	10	0.011	161	0.114	10.4:1

Size and Years-in-Ocean of Adult Experimental Fish

Since transported fish (chinook salmon and steelhead) had the opportunity to enter the ocean more than 1 mo earlier than control fish that migrated naturally, the size and ocean age of returning adults were examined to determine whether a difference existed. The average weights of chinook salmon and steelhead released as controls were compared with the average weights of transported groups returning at the same ocean age. A paired comparison t-test using the data from Table 9 showed no significant differences in average weights for chinook salmon and steelhead (chinook salmon: $t = 0.315, P>0.5$; steelhead: $t = 0.297, P>0.5$ df = 8).

The ratio of age .3 to age .2 chinook salmon and the ratio of age .2 to age .1 steelhead were compared (Table 10) between transported and control groups. These comparisons indicated whether transporting affected the time that fish spent in the ocean before their return to Little Goose Dam. An analysis of variance of the ratios for the 3 yr of the study (Table 11) showed that the differences in ocean age between transported and control steelhead were not significant ($P<0.05$). A significant ($P<0.05$) difference in ocean age between control and transported chinook salmon did occur with a slightly higher ratio of .3/.2-age chinook salmon indicated among control returns. By these analyses, the transportation of smolts to locations downstream from Bonneville Dam was not shown to influence either the age or size of returning adult steelhead but may have influenced age of returning adult chinook salmon.

TABLE 9.—Average weights (kilograms) of returning chinook salmon and steelhead to Little Goose Dam from control (C) and transported (T) releases of smolts, 1971-73.

Species and year of release	Jacks		2-yr-in-ocean fish		3-yr-in-ocean fish	
	C	T	C	T	C	T
Chinook salmon:						
1971	1.66	1.40	5.06	4.74	8.22	9.20
1972	1.41	1.39	4.19	4.28	10.08	9.27
1973	1.86	1.51	4.40	4.46	7.77	9.02
Steelhead:						
1971	2.42	2.37	5.80	5.16	6.19	5.75
1972	2.39	2.53	4.38	4.24	4.44	4.84
1973	2.32	2.25	4.47	4.73	3.74	4.70

TABLE 10.—Comparison of transport and control age ratios on adults returning to Little Goose Dam, 1971-73. Chinook salmon age .3/.2 and steelhead age .1/.2 were used to determine ratios.

	Control			Transported		
	Ocean age[1] (no.)			Ocean age[1] (no.)		
Year	.2	.3	Ratio	.2	.3	Ratio
Chinook salmon:						
1971	28	19	0.68	153	93	0.61
1972	12	9	0.75	48	32	0.67
1973	11	7	0.64	272	161	0.59
	.1	.2		1	.2	
Steelhead:						
1971	75	121	1.61	290	524	1.81
1972	75	57	0.76	389	269	0.69
1973	21	41	1.95	628	629	1.00

[1]Age designation follows the formulas of Koo (1962). The number of years at sea is shown by an Arabic numeral preceded by a dot.

TABLE 11.—Analysis of variance of ratios of ocean age .3 to .2[1] chinook salmon and age .2 to .1 steelhead adults returning to Little Goose Dam from transported and control releases.

Species	Source	df	SS	MS	F
Chinook salmon	Treatments (transport and controls)	1	0.00657	0.00657	23.6*
	Years (1971-73)	2	0.00931	0.00465	33.3*
	Error	2	0.00394	0.000197	
	Total	5	0.016274		
Steelhead	Treatments (transport and controls)	1	0.114	0.114	0.633NS
	Years (1971-73)	2	1.058	0.529	2.94NS
	Error	2	0.359	0.180	
	Total	5	1.532		

*$P<0.05$.

[1]Age designation follows the formulas of Koo (1962). The number of winters at sea is shown by an Arabic numeral preceded by a dot.

Recovery of Marked Chinook Salmon in the Commercial and Sport Fisheries

The experimental plan to evaluate recoveries of adult chinook salmon in the commercial, Indian, and sport fisheries required sampling of these fisheries each year from 1973 to 1975. However, the spring chinook salmon run began a rapid decline in 1973, which forced the commercial fishery to close in 1974 and 1975. As a consequence, sufficient data on chinook salmon were obtained only in 1973 for comparison of transported and control recoveries. A test fishery was conducted in 1974 and 1975, but only 18 salmon were recovered from the experimental releases during these years—too few to make comparisons of recoveries. Sixty-one salmon (Table 12) were recovered in 1973 from the 1971 experimental releases. The combined transport/control ratio of these recoveries, computed after adjusting the number of juveniles released, indicated that chinook salmon transported as juveniles were captured at 2.86 times the rate of control fish. This is a substantially higher test/control ratio than the 1.6:1 computed for returns to Little Goose Dam, indicating that transported groups were captured at a higher rate in the fishery than at Little Goose Dam. This

TABLE 12.—Comparison between transported and nontransported (control) chinook salmon of 1971 that were captured during 1973 as adults in the commercial, Indian, and sport fisheries in the lower Columbia River. (Numbers observed, not estimated.)

Item	Transported: Dalton Point Recaptures No.	Transported: Dalton Point Recaptures %	Transported: Bonneville Dam Recaptures No.	Transported: Bonneville Dam Recaptures %	Control Recaptures No.	Control Recaptures %
Upstream from Bonneville Dam (Indian fishery)	14	0.046	14	0.040	4	0.019
Downstream from Bonneville Dam (commercial and sport fisheries)	9	0.029	18	0.051	2	0.010
Total	23	0.075	32	0.091	6	0.029
Combined recoveries (Dalton Point and Bonneville Dam)[1]				0.083	6	0.029

[1]Transport/control ratio = 2.86:1.

suggests that perhaps the adult fish from transported stocks were spending a longer time in the lower river, thus allowing a greater catch of these groups.

Recovery of Marked Steelhead in the Indian and Sport Fisheries

The Indian fishery of the lower Columbia River in 1973 and 1974 was not sampled because of closures during most of the season. However, in 1975 a substantial fishery was in progress. Sampling of this fishery yielded 39 marked steelhead from 1973 experimental releases. Thirty-eight of these were from transported groups; only one fish of a control group was recovered. The ratio of transport to control was 30:1, again indicating a higher catch rate of transported steelhead in 1973 than was recorded at Little Goose Dam where the transport/control ratio was 13.4:1.

TABLE 13.—Recoveries of adult steelhead from the sport fishery upstream from Little Goose Dam. Juveniles were released, 1971-73, as controls at Central Ferry; transported groups were released at Dalton Point and Bonneville Dam.

Year released	Control: No. of fish	Control: Percentage return	Transported groups: No. of fish	Transported groups: Percentage return	Transport/control ratio[1]
1971	50	0.150	149	0.184	1.2:1
1972	24	0.074	63	0.126	1.7:1
1973	0	—	24	0.037	—
Total	74		236		

[1]Transport/control ratios computed from the combined recoveries of the Bonneville Dam and Dalton Point releases.

The sport fishery upstream from Little Goose Dam in the Snake River was intensive in 1972 and 1973 but was closed for a portion of 1974. Sampling of this fishery yielded 310 marked steelhead (Table 13) from experimental releases in 1971-73. The transport/control ratio estimated from these recoveries indicated a benefit from transport, but the benefit was about half that indicated downstream at Little Goose Dam from releases in 1971 and 1972. The benefit was substantial in all recovery locations from releases in 1973.

Returns of Adult Experimental Fish to Hatcheries and Spawning Grounds

Spawning ground surveys and examination of adult fish in Idaho hatcheries provided further information concerning transport/control ratios of chinook salmon and steelhead at their "home" destination.

Adult chinook salmon returns were examined at Rapid River Hatchery; steelhead returns were examined at Dworshak National Fish Hatchery and at the Pahsimeroi Hatchery (Table 14). Ex-

TABLE 14.—Returns of adult chinook salmon and steelhead to hatcheries of the upper Snake River drainage, 1971-73.

Species and hatchery of origin	Release site and experimental group[1]	Released 1971: Recoveries No.	Released 1971: Recoveries %	Released 1971: Transport/control ratio	Released 1972: Recoveries No.	Released 1972: Recoveries %	Released 1972: Transport/control ratio	Released 1973: Recoveries No.	Released 1973: Recoveries %	Released 1973: Transport/control ratio
Chinook salmon Rapid River	Bonneville Dam (T)	33	0.094	4.95:1	5	0.009	—	24	0.029	14.5:1
	Dalton Point (T)	25	0.082	3.32:1	7	0.014	—	42	0.073	36.5:1
	Total	58	0.088	4.63:1	12	0.011	—	66	0.047	23.5:1
	Central Ferry (C)	4	0.019		0	0	—	2	0.002	
Steelhead Dworshak	Bonneville Dam (T)	96	0.214	1.37:1	26	0.095	3.80:1	104	0.283	13.5:1
	Dalton Point (T)	49	0.136	0.87:1	17	0.074	3.00:1	114	0.428	20.4:1
	Total	145	0.179	0.87:1	43	0.086	3.44:1	218	0.344	16.4:1
	Central Ferry (C)	52	0.156		8	0.026		9	0.021	
Pahsimeroi	Bonneville Dam (T)	8	0.018	—	11	0.040	3.33:1	18	0.049	24.5:1
	Dalton Point (T)	5	0.014	—	9	0.039	3.25:1	18	0.068	34.0:1
	Total	13	0.016	—	20	0.040	3.33:1	36	0.057	28.0:1
	Central Ferry (C)	0			4	0.012		1	0.002	

[1]T = transported group; C = control.

cept for steelhead returns to Dworshak Hatchery from releases in 1971, transport/control ratios computed from these data indicated that the benefits from transportation were greater than those indicated from returns to Little Goose Dam.

This was particularly evident in returns of chinook salmon and steelhead from releases in 1973. At Little Goose Dam the combined transport/control ratio was 15.4:1 for chinook salmon and 13.4:1 for steelhead; the ratios at the hatcheries were 23.5:1 for chinook salmon (Rapid River Hatchery) and 16.4:1 (Dworshak) and 28:1 (Pahsimeroi) for steelhead. One possible reason for the difference might be a differential in benefit which favored hatchery stocks. Because returns to Little Goose Dam were a mixture of hatchery and wild stocks, the proportion of each stock in a sample could alter the transport/control ratio.

Spawning ground surveys for adult chinook salmon were conducted in 1972, 1973, 1975, and 1976. No surveys were made in 1974 because of the small number of marked fish available for recovery. The location of streams surveyed was identical to that described by Ebel et al. (1973). Fourteen marked fish were recovered during the 4 yr of surveys. Of these, 12 were identified as having been released as transports and 2 as controls. Although the recoveries of adults on the spawning grounds were very low, recoveries at Rapid River Hatchery were substantial (Table 14). The fact that 12 adult fish, transported as juveniles from Little Goose Dam, were recovered on the spawning grounds indicates that transported wild stocks as well as hatchery stocks continued their upstream migration after leaving Little Goose Dam.

Straying of Experimental Groups

The chinook spawning grounds of the Okanogan and Methow Rivers and other spring chinook hatcheries in the Columbia River drainage were checked to determine if adult returns from release groups had "strayed" to spawning locations other than their parent stream or hatchery. No strays were indicated in checks of hatcheries and spawning areas in the Columbia River above the mouth of the Snake River, but a few strays (16 chinook salmon and 3 steelhead) were recovered at Pelton Dam on the Deschutes River in Oregon. Of the 16 chinook salmon recovered, 10 were from groups transported as juveniles, 2 from controls, and the remaining 4 could not be positively identified as to release group because tag codes were lost. The three steelhead recovered were also from groups transported. These recoveries indicate that the homing behavior of a portion of the chinook salmon transported as juveniles may have been adversely affected. However, the proportion of the transported groups affected to this degree must have been small; 857 chinook salmon and 2,720 steelhead were identified at Little Goose Dam from the same release groups. The homing behavior of these fish obviously was not damaged. Additional data are needed to quantify the degree of straying that occurs from transporting steelhead and chinook salmon from Little Goose Dam.

DISCUSSION

Comparison of Results With Other Studies

The results of this study are similar to an earlier study done by Ebel et al. (1973) in which survival was definitely increased by transporting the fish downstream as juveniles. Percentage returns of adults to Little Goose Dam from transported fish were greater than that from control fish for the Dalton Point as well as the Bonneville Dam release sites for all 3 yr. However, the estimated percentage returns of chinook salmon were much lower than those reported by Ebel et al. (1973) when fish were collected and transported from Ice Harbor Dam in 1968. Estimated returns of adult chinook salmon, transported as juveniles from Ice Harbor Dam, ranged from 4.3 to 9.0%; whereas, returns of adult chinook salmon, transported as juveniles from Little Goose Dam in this study, ranged from 0.11 to 0.78%—substantially lower than achieved at Ice Harbor Dam.

There are several factors which could have caused the lower percentage returns from Little Goose Dam: 1) some homing ability may have been lost because the fish were intercepted and transported from a location about 130 km farther upstream; 2) the fish collected at Ice Harbor Dam may have been more hardy individuals because they migrated a greater distance, which would have allowed more of the weaker individuals to be eliminated from the populations; 3) the stocks collected at Ice Harbor Dam in 1968 were primarily wild stocks and thus hardier—more able to stand the stress of handling, marking, and hauling; or 4) the general condition of the fish at the time of marking may have been better because the collection, handling, and hauling system used at Ice

Harbor Dam could have resulted in less stress than that at Little Goose Dam. Further examination of the data, however, implies that the condition of the fish (factor 4) may have been the main factor. Estimated adult returns of chinook salmon to Ice Harbor Dam from fish transported in 1969 and 1970 (Slatick et al. 1975) were much lower (0.113-0.581%) than recorded from experimental groups released in 1968. The authors attributed the lower returns to stress caused by the placement of two new dams (Lower Monumental and Little Goose) in the migratory path of the juveniles and from stress caused by the use of a fish pump in the handling operation. The descaling and delayed mortality percentages in the study at Little Goose Dam indicated that stress in the collection, handling, and hauling procedures was a factor.

Steelhead were not affected in the same manner as chinook salmon in either this study or the earlier studies at Ice Harbor Dam. In both studies steelhead returned at a substantially higher rate than chinook salmon. Estimated percentage returns to Little Goose Dam of steelhead that had been transported as juveniles ranged from 1.4 to 2.6%; returns from releases at Ice Harbor Dam in 1969 and 1970 ranged from 0.6 to 1.6%. Since steelhead smolts are larger than chinook salmon smolts, they may have been able to withstand the rigors of collection, handling, and marking; the very low delayed mortality percentages, shown in this study for steelhead, support this reasoning.

Effect of Transportation on Homing

The transport/control ratios provide information on the effect of transportation on homing. For example, if no differential mortality occurred between groups, a steadily decreasing ratio of transport/control numbers from the commercial and sport fisheries below Bonneville Dam to the spawning ground would indicate a loss of homing ability or straying.

During the 3 yr of study, this type of comparison could only be made from 1971 releases of juvenile chinook salmon because the lower river commercial fishery was closed after 1973. A comparison of recovery ratios of adult fish from these releases showed that the transport to control ratios were 2.86, 1.65, and 3.95:1 in the commercial fishery at Little Goose Dam and the spawning grounds,[14] respectively. Although there was a variation in the ratios from the lower river to the spawning grounds, these ratios indicated that ability of transported chinook salmon to home to either their parent stream or Rapid River Hatchery was not seriously damaged by transporting the fish around the seven dams and reservoirs between Little Goose and Bonneville Dams.

The ratios also imply that hatchery stocks were benefited to a greater degree than wild stocks. When returns to the spawning grounds were separated from returns to Rapid River Hatchery and separate transport/control ratios were computed, the ratio for wild stocks became 1.5:1 and hatchery stocks, 4.6:1. However, more data are needed regarding this aspect (only six fish were recovered on the spawning grounds from releases in 1973) before conclusions can be made on the differential effect that transportation might have on hatchery and wild stocks of chinook salmon. A comparison between the ratio in the commercial fishery (2.8:1) and at Little Goose Dam (1.6:1) also indicates that transported chinook salmon may have been affected differently from controls—if one assumes that no differential mortality occurred between control and transported fish as they moved upriver and that wild and hatchery stocks were captured at the same rate in the fishery as they were at Little Goose Dam. Returning adults transported as smolts may have been slightly disoriented or remained for a longer period in the lower river, thus permitting the fishery to take a disproportionate number of transported fish.

Ebel et al. (1973) found no difference in transport/control ratios from the commercial fishery to the spawning grounds when data from releases at Ice Harbor Dam in 1968 were analyzed.

Disproportionate straying of adults from groups transported as juveniles would also be an indication that homing behavior had been affected by the transportation. No straying of either chinook salmon or steelhead was observed in the earlier study at Ice Harbor Dam. On the basis of recoveries of marked chinook salmon in the Deschutes River, some straying of chinook salmon that had been transported as juveniles occurred in this study. This instance of straying and the variations of transport/control ratios from the fishery to Little Goose Dam indicate that the migratory route lost by collecting the juveniles 130 km upstream at Little Goose Dam may be of some importance in determining homing behavior. A current

[14]Return to the hatcheries included in computation of transport/control ratio.

study (Park[15]) being conducted at Lower Granite Dam (about 200 km upstream from Ice Harbor Dam) by NMFS should provide further information on this subject. Preliminary data obtained from adult steelhead and chinook salmon returning to Lower Granite Dam show that transport/control ratios (2.5-2.7:1) obtained from experiments in 1975 and 1976 are similar to those obtained at Little Goose Dam. Insufficient data are available at this writing to determine variations in ratios from the lower river to the estuary or to determine degree of straying.

SUMMARY AND CONCLUSIONS

The main objectives of the research at Little Goose Dam were to determine the effect of transportation on homing and survival of juvenile chinook salmon and steelhead collected at Little Goose Dam and released downstream and to compare these results with an earlier study done at Ice Harbor Dam where fish were transported a shorter distance. The data clearly show that homing ability was not seriously diminished in either chinook salmon or steelhead, and that survival of both species was increased by transporting the fish to release locations downstream from Bonneville Dam.

A comparison of the results of this study with an earlier study done by Ebel et al. (1973) and by Slatick et al. (1975) at Ice Harbor Dam indicates that the effect of collecting the fish about 130 km farther upstream did not seriously diminish their homing ability in comparison with homing ability obtained in the experiment at Ice Harbor Dam. The increases in survival of transported fish noted in the study at Little Goose Dam were also similar to those noted at Ice Harbor Dam, but estimated percentage return of chinook salmon was substantially lower than that achieved at Ice Harbor Dam. Observations made throughout the study indicated that chinook salmon returns might be increased by reducing injury or stress during diversion, collection, and handling process.

The main conclusions bearing on the effect of transporting juveniles from Little Goose Dam to release locations downstream from Bonneville Dam were:

1) Analysis of transport/control ratios obtained from returning adults indicated that returns from naturally migrating juvenile chinook salmon and steelhead that were transported from Little Goose Dam to release locations downstream from Bonneville Dam were increased from 1.1 to 15 times in the fishery and to Little Goose Dam.

2) A significant ($P<0.01$) difference in benefit from transportation was noted between chinook salmon and steelhead; the greatest return and, hence, the greatest benefit occurred with steelhead.

3) Homing of adult fish that had been collected as juveniles at Little Goose Dam and transported several hundred kilometers downstream to Bonneville Dam apparently was not seriously diminished although a small portion ($P<0.02\%$) of the transported adult chinook salmon was known to have strayed.

4) There was no significant ($P<0.05$) difference in adult returns from two release sites tested (Dalton Point and Bonneville Dam) of either steelhead or chinook salmon.

5) Timing of migration of juvenile migrants was not related to timing of adult returns to Little Goose Dam.

6) Neither size nor ocean age of adult steelhead transported experimentally as juveniles was significantly ($P<0.05$) different from controls. Thus transporting the fish did not appear to affect either size or age of returning adult steelhead.

7) Although size of adult chinook salmon transported as juveniles was not significantly ($P<0.05$) different from controls, ocean age was. Transportation, therefore, may have influenced ocean age of returning adult chinook salmon.

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IS OVULATION IN DOLPHINS, *STENELLA LONGIROSTRIS* AND *STENELLA ATTENUATA*, ALWAYS COPULATION-INDUCED?

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ABSTRACT

This study of 58 nonpregnant uteri and ovaries of the spinner dolphin, *Stenella longirostris*, and the spotted dolphin, S. attenuata, was undertaken to ascertain whether ovulation is copulation-induced (reflex) or occurs spontaneously. Control specimens of immature, pregnant, and lactating females were examined also and were used to define the normal reproductive events in uteri and ovaries of these species. No differences were found between the two species. In about one half of the specimens we found active corpora lutea of recent origin and in another 15% of *S. attenuata* and 29% of *S. longirostris*, corpora had fibrous centers but were hormonally active. No embryos were found and the endometrial changes were such that early but unobserved pregnancies could be excluded. In 35% of the specimens from *S. attenuata* the macroscopic diagnosis of corpus luteum was erroneous, while this was true of 21% in *S. longirostris*. The corpora were degenerating and more resembled early corpora albicantia histologically. In two of these specimens, endometritis was found and the endometrial histology gave evidence of abortion in three. These findings are evidence that these *Stenella* species may sometimes ovulate spontaneously and that macroscopic classification of corpora lutea in the past may frequently have been erroneous.

The reproductive physiology of the spotted dolphin, *Stenella attenuata*, and spinner dolphin, *S. longirostris*, has not been fully elucidated. In particular, it is presently unknown whether these dolphins ovulate spontaneously or on reflex after copulation. Some reasons to believe the latter have been presented for *Tursiops truncatus* (Harrison 1977) and the same is implied for other Cetacea. The finding of corpora lutea almost exclusively in pregnant animals is the basis for this assumption, and the purpose of this study is to examine the genital tracts of 58 nonpregnant animals with corpora lutea in detail in an attempt to resolve this question. In a detailed study of spotted dolphin, Perrin et al. (1976) found that of 242 females with corpora lutea, 229 (95%) were pregnant. In a similar study of spinner dolphins, Perrin et al. (1977) found that 2.8% of 536 adult females contained corpora lutea whose presence could not be explained by pregnancy, lactation, or abortion.

The distribution of species with and without reflex ovulation has been reviewed by Jöchle (1973). A surprisingly large number of species is listed as having exclusively or predominantly reflex ovulation, including Cetacea. Only primates, mouse and rat are cited as exceptions; however, modern studies suggest this to be an incomplete list. In several papers on Camelidae, reflex ovulation is well supported by experimental studies and by observations from abatoirs. Although camels and their South American relatives must be accepted as being reflex ovulators, the carefully controlled study by England et al. (1969) showed that "occasional spontaneous ovulation occurred during the height of the breeding season" in the llama, *Lama glama*.

In an attempt to gain additional information on the reproductive physiology of *S. longirostris* and *S. attenuata*, we examined the reproductive tracts of animals recorded to possess corpora lutea while not pregnant. Special attention was paid to ascertaining any reasons for the existence of these corpora lutea, such as early undetected pregnancy and an attempt was made to correlate the ovarian status with endometrial changes.

MATERIALS AND METHODS

Reproductive tracts of female *S. longirostris* and *S. attenuata* were collected at sea by observers during commercial tuna fishing operations in the southeastern Pacific Ocean (Perrin et al. 1976,

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1977). The organs were preserved in 10% Formalin[4] (Mallinkrodt) solution and stored at the Southwest Fisheries Center (SWFC), National Marine Fisheries Service, NOAA, La Jolla, Calif. At the time of capture, a variety of observations were recorded, including identified pregnancy, size of the fetus, and lactation. These data, dates and location of capture as well as related pertinent information, are recorded in logs at SWFC. Here also the ovaries were sliced at 1 mm intervals, and observations such as the presence of corpora lutea, corpora albicantia, and ovarian size were recorded and correlated with capture information. Those apparently gravid uteri whose ovaries had a corpus luteum were dissected further and, occasionally, small fetuses were identified by SWFC staff. In addition, the present authors carefully dissected three intact uteri of the 1977 catches where ovaries contained corpora lutea but in which pregnancy had not been recorded.

For the purpose of the present study the reproductive tracts of 53 nonpregnant dolphins, captured in 1976, and whose ovaries were recorded to contain corpora lutea, were examined in detail. A few specimens of 1975 and 1977 were also studied and are included, bringing the figure to 58 genital tracts. The tabulation of the reproductive condition of these tracts is shown in Table 1.

These specimens represent the majority of reproductive tracts recorded to possess unexplained corpora lutea in 1976. There were 67 in all but not all of the specimens were in suitable condition for inclusion in this study. Thus, several were too severely autolyzed for proper evaluation; in others, either the complete ovaries or uteri could not be located in the specimen collection.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Reproductive tracts of *Stenella* spp. studied because corpora lutea were found in the absence of pregnancy or lactation.

Species	1975	1976	1977
Stenella longirostris	0	38	0
S. attenuata	2	15	3

In an effort to better understand the macroscopic and histologic features of dolphins with known reproductive events, it was desirable to select suitable control material from the same stored collection. Six groups of specimens were selected for this purpose and consisted of the following specimens: Group I, 3 tracts of immature *S. longirostris*; Group II, 6 tracts of mature female *S. longirostris* having no corpus luteum and, therefore, termed "resting"; Group III, 12 tracts of *S. longirostris* with early pregnancy, the embryos measuring from 1 to 53 mm long (1-5 g with placenta); Group IV, 6 tracts of later pregnant dolphins (4 *S. longirostris* and 2 *S. attenuata*) with fetal sizes ranging from 300 to 725 mm; Group V, 11 tracts of lactating, nonpregnant females (10 *S. longirostris* and 1 *S. attenuata*); Group VI, the experimental group, 58 tracts of nonpregnant females possessing a corpus luteum (38 *S. longirostris* and 20 *S. attenuata*; Table 1); for a total of 96 female genital tracts.

The gross examination of genital tracts by us ascertained the following standard information: Weight; length and width of uterine horns and cervices; thickness of uterine walls at standard locations. Histologic sections, stained with hematoxylin and eosin, were prepared from standard locations of tubes, uterine horns, lower uterine segments, and ovaries (Figure 1). Measurements of uterine mucosa and muscularis were made at low power microscopic examination with the aid of a calibrated ocular micrometer. At histologic examination the uterine findings (glands, secretion, mitoses, edema, hyalinization, inflammation) were compared with the ovarian activity. Relevant photomicrographs were made with a Zeiss Axiomat.

RESULTS

Controls

Group I, Immature Females

These three *S. longirostris* measured from 164 to 176 cm body length (Table 2) and possessed neither

TABLE 2.—Group I: Immature controls, *Stenella longirostris* captured on 20 February 1976.

Specimen no.	Dolphin length (cm)	Uterus weight (g)	Left horn of uterus				Right horn of uterus			
			Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)
1	176	47	10	1.49	0.60	0.54	9	2.09	0.75	0.60
2	168	44	9	1.34	0.39	0.60	9	1.07	0.36	0.62
3	164	22	9	1.10	0.60	0.42	7	1.07	0.36	0.54
			Average	1.31	0.53	0.52		1.41	0.59	0.58

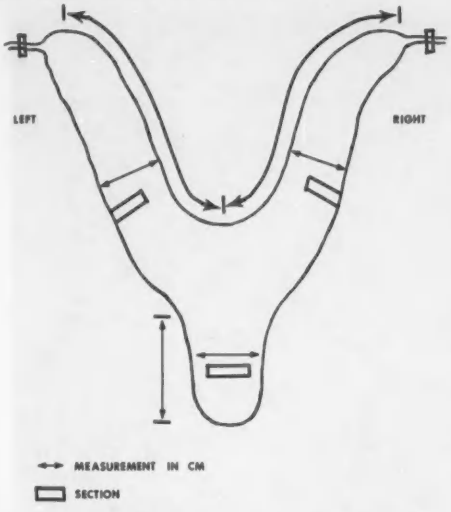

FIGURE 1.—Diagram of dolphin uterus. Arrows indicate measurements taken in *Stenella* spp. and squares denote location of histologic sections.

corpora lutea nor corpora albicantia. Because of their size it was assumed that they were at the verge of maturity. As shown in Figure 2, uterine horns were of equal size, there were no stretch marks and the endometrium was flat. Numerous Graafian follicles of varying stages of development were present in both ovaries, but there was no evidence of ovulation. The endometrium was thin and composed of tubular glands possessing neither secretion nor mitoses; the stroma was devoid of inflammation and edema or hyalinization (Figure 3). The fallopian tubes were small and empty. In all subsequent specimens, slides of fallopian tubes were examined. No relevant changes were observed and they are therefore not described further. Also, sections of the lower uterine segment were found to make no contribution in the assessment of reproductive state and are not included in this analysis.

Group II, Mature Females

These six *S. longirostris* measured from 173 to 186 cm in length and were adjudged to be mature

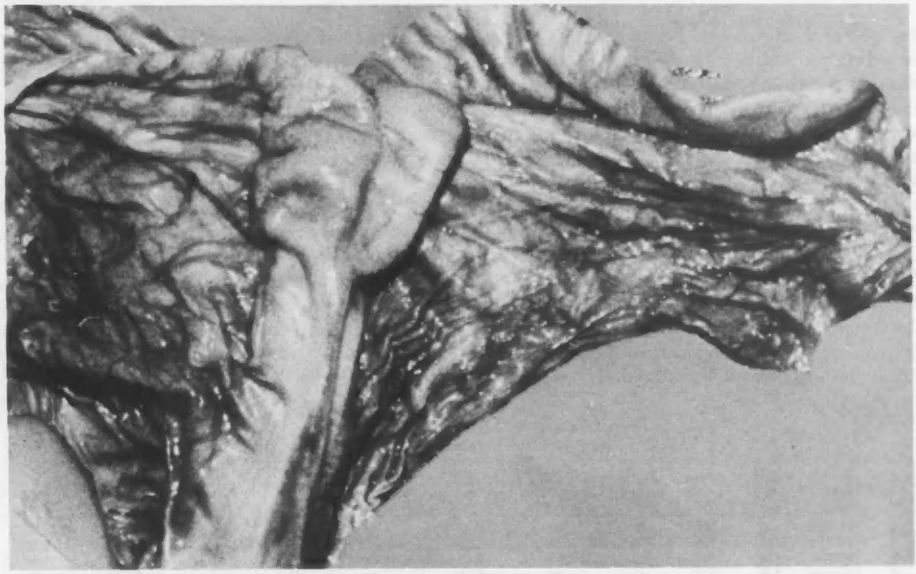

FIGURE 2.—Immature uterus of *Stenella longirostris* (no. 1, Table 2). Note the flat folds of endometrium, equal-sized horns, and lack of serosal stretch marks (center)

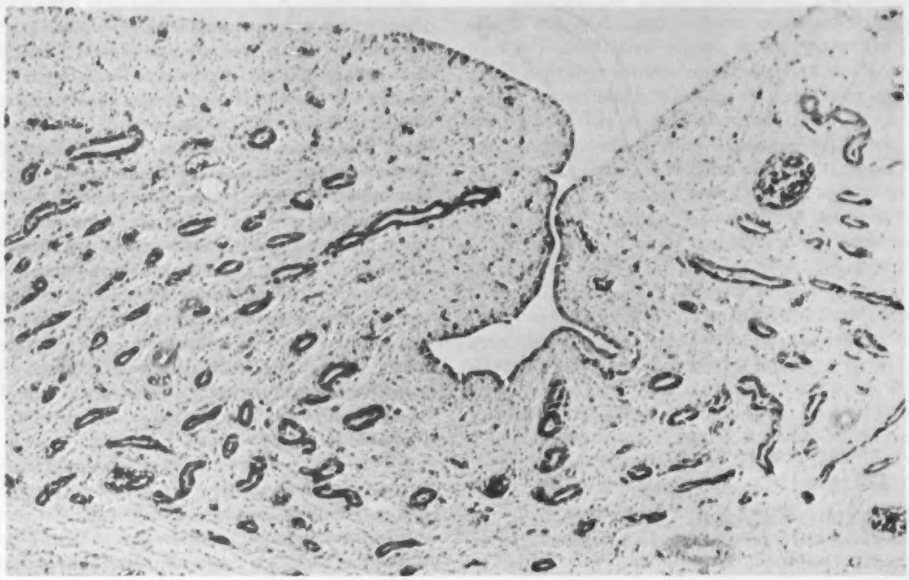

FIGURE 3.—Endometrium of immature *Stenella longirostris* (no. 3, Table 2). Tubular glands, little folding, thin endometrium, no secretion or mitoses (hematoxylin and eosin × 60).

because of their size and the presence of at least one corpus albicans. They were not lactating nor did they possess a corpus luteum. The appropriate measurements are set forth in Table 3. In general, the horns were asymmetrical but not so markedly as those of lactating females (Group V), with the exception of specimen no. 4 (Table 3). The wrinkled serosa and congestion of endometrium of this animal's left horn indicated recent pregnancy (Figure 4). All but one female of this group had "stretch marks" which we assumed to be an indication of previous pregnancy. Microscopic study of the corpora albicantia in this group allowed some correlation with the endometrial findings. Thus, the apparently most recently delivered uterus (Figure 4) had a still cellular corpus albicans (Figure 5) and, inflammatory cells, hemosiderin macrophages and stromal hyalinization were observed in the congested endometrium (Figure 6). In the others, judged to have had past pregnancies, the corpus albicans was less cellular, more hyalinized and shrunken. The endometrium did not appear to be stimulated, had thin epithelium, no mitoses but scattered macrophages were in the process of removing debris. Apparently later still, Graafian follicle development commences, uterine horns are of nearly equal size and endometrial glandular redevelopment occurs with mitoses, glandular convolutions, occasional epithelial vacuoles, and stromal edema (Figure 7).

TABLE 3.—Group II: Mature controls, *Stenella longirostris*, for 1976.

Specimen no.	Month of capture	Dolphin length (cm)	Uterus weight (g)	Left horn of uterus				Right horn of uterus			
				Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)
1	February	186	108	13	1.79	0.75	1.49	10	1.94	0.66	1.49
2	February	181	123	17	2.70	0.75	1.04	15	2.24	0.90	0.90
3	February	179	136	13	1.79	0.66	1.19	11	1.19	0.75	1.64
4	February	178	152	17	2.99	0.90	2.39	8	4.78	0.90	1.94
5	July	175	98	16	1.64	0.30	0.90	18	1.49	0.60	1.49
6	June	173	110	23	4.18	0.90	1.49	18	3.58	1.04	1.49
				Average	2.52	0.71	1.42		2.54	0.81	1.49

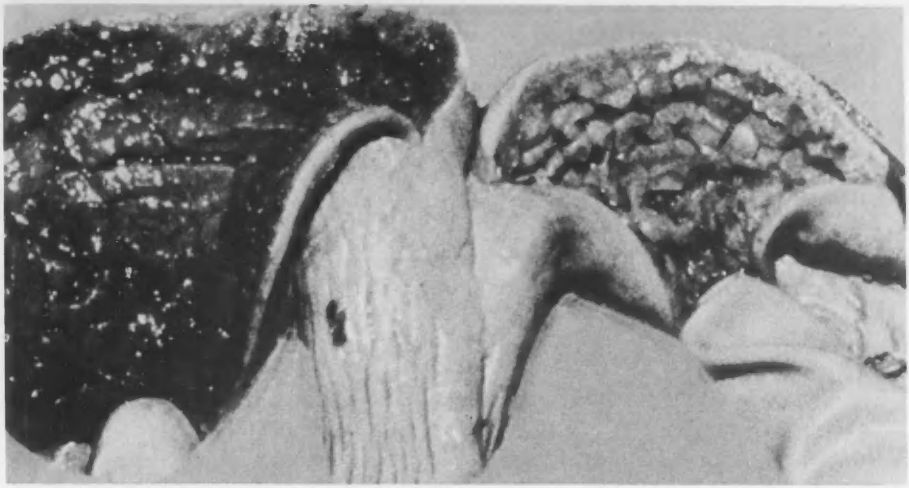

FIGURE 4.—Mature animal's uterus, presumably recently delivered (no. 4, Table 3). Note larger left horn with congestion and serosal stretch marks.

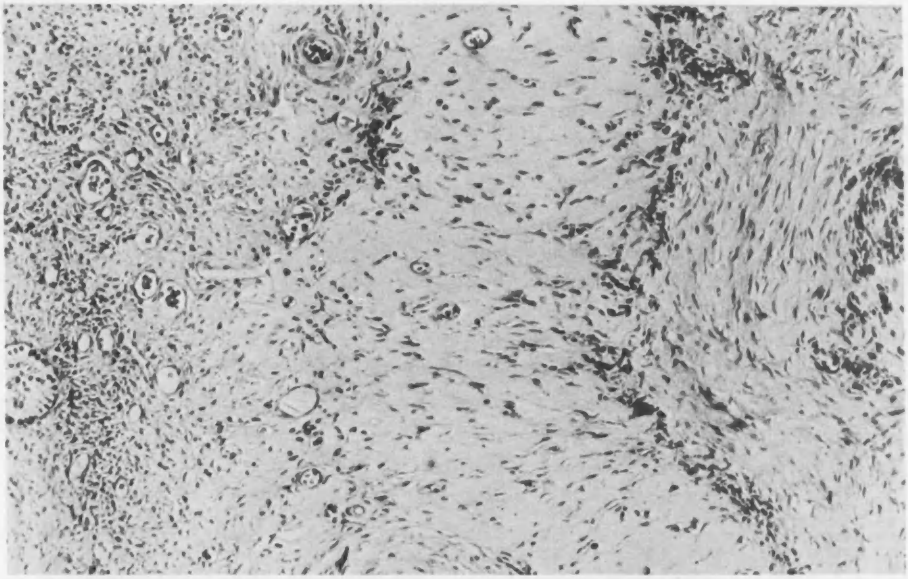

FIGURE 5.—Corpus albicans of animal in Figure 4. At right is former follicular cavity, replaced by young fibroblastic tissue. Dark cells in central (former luteal) band of corpus albicans suggest recent conversion of corpus luteum to corpus albicans (hematoxylin and eosin × 120).

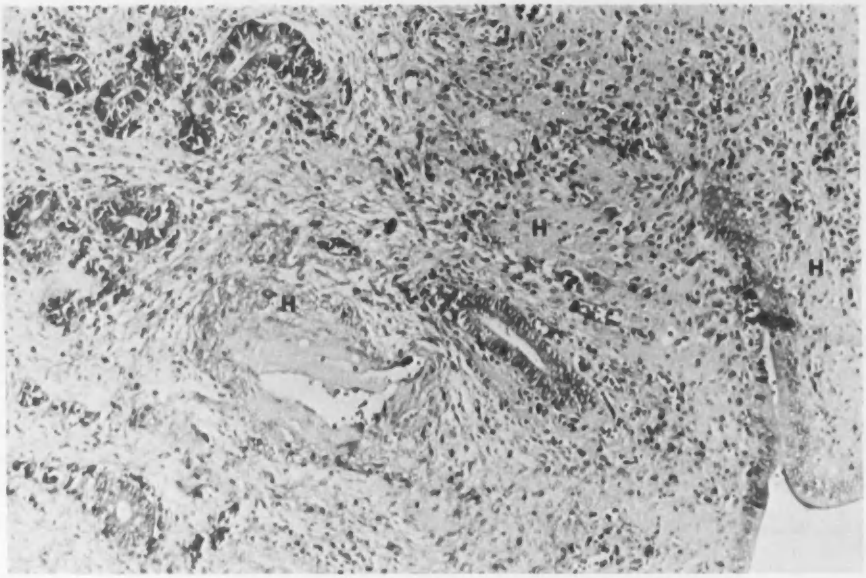

FIGURE 6.—Endometrium of animal in Figures 4 and 5, surface at right. Infiltration of stroma with macrophages; sparse glands; hyalinization of stroma and larger vessel walls at H (hematoxylin and eosin × 120).

Group III, Early Pregnancy

There were 12 *S. longirostris* in this group measuring from 166 to 188 cm in length (Table 4). With the exception of the first specimen listed, the left uterine horn was the larger. In this exceptional animal, the corpus luteum was also on the right and no corpus albicans was found in the left side. Uterine size and weight did not correlate well with embryonic size (1-53 mm) or weight (1-5 g). The embryos had been removed previously and their placentas had apparently not yet implanted. The larger (pregnant) horn had a congested endometrium and distended lumen (Figure 8).

This is an important control group for the experimental Group VI whose uteri were empty despite the presence of a corpus luteum. Thus, it is noteworthy that even in small embryos (Figure 9) the placental membranes are of appreciable size and they grow rapidly (Figure 10) so that they are not easily overlooked in dissections. Early limb bud development could be recognized in embryos sized 5 mm or more.

TABLE 4.—Group III: Early pregnant controls, *Stenella longirostris*. All from February 1976 except no. 11 captured in May 1976.

Specimen no.	Dolphin length (cm)	Uterus weight (g)	Left horn of uterus				Right horn of uterus				Fetus	
			Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (mm)	Weight (g)
1	176	140	10	6.87	1.49	1.49	15	5.37	1.49	1.49	1	1
2	172	171	20	—	—	—	12	5.67	1.19	1.49	2	1
3	178	145	15	5.07	0.90	1.49	12	4.03	1.04	1.94	2	1
4	181	208	28	2.69	1.19	0.96	20	2.69	0.90	0.78	5	1
5	188	163	20	2.83	0.75	0.04	15	2.99	0.75	1.04	5	2
6	172	192	19	5.97	1.19	1.04	12	6.87	1.79	1.49	5	2
7	166	204	17	6.87	0.75	0.90	11	7.46	1.34	0.75	5	2
8	176	212	25	5.37	1.49	1.04	15	3.88	0.60	1.19	5	2
9	167	227	19	6.87	1.19	1.94	13	—	2.39	1.49	5	2
10	184	229	28	2.09	0.36	1.04	15	3.58	0.90	1.19	5	2
11	180	144	17	4.78	1.19	1.04	13	2.99	1.19	1.19	8	2
12	180	187	23	1.04	0.35	0.90	16	2.09	0.30	0.90	53	5
			Average	4.68	0.99	1.17		4.33	1.16	1.25		

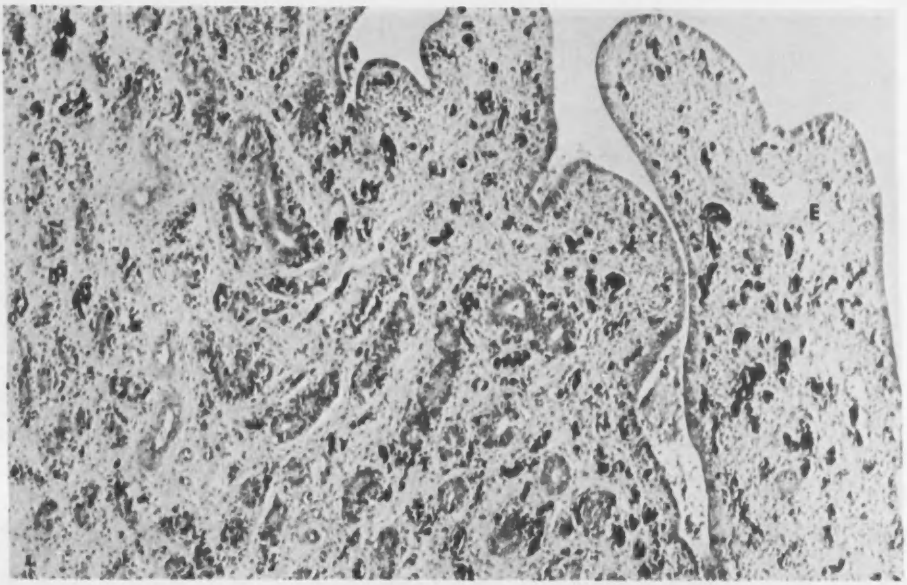

FIGURE 7.—Endometrium undergoing early stimulation, presumably after past pregnancy (no. 3, Table 3). Glands are more numerous and coiled. They contain occasional epithelial secretory vacuoles and mitoses. Focal edema (E) of stroma commences (hematoxylin and eosin × 60).

FIGURE 8.—Early pregnant uterus with distended left horn and hyperemia of endometrium (no. 4, Table 4).

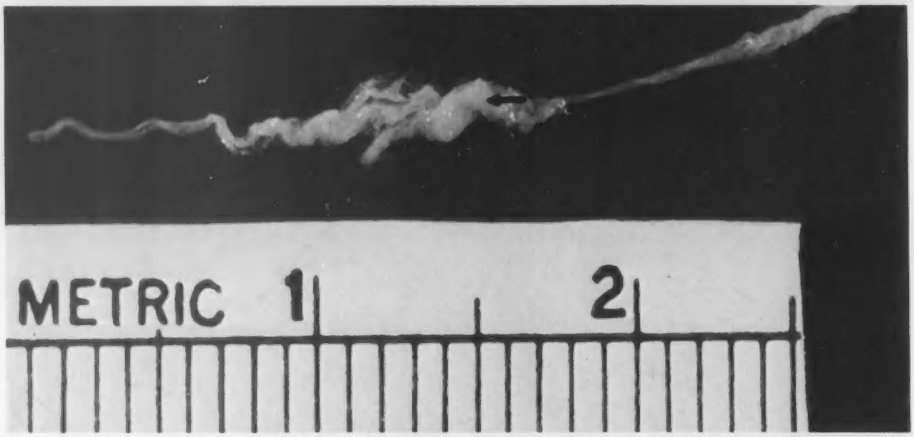

FIGURE 9.—Smallest (2 mm) normal embryo at arrow with long, filmy placental membranes (no. 3, Table 4).

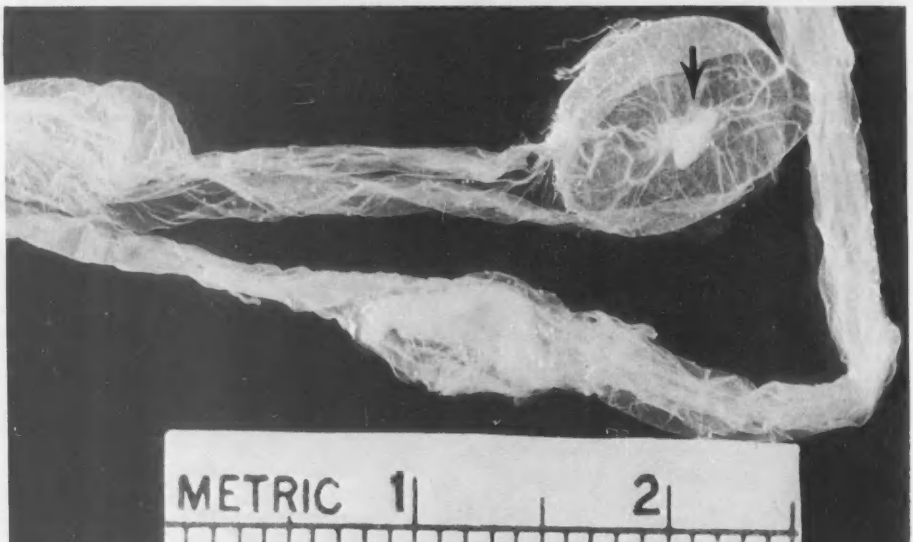

FIGURE 10.—Five mm embryo (arrow) with huge placental membranes (no. 9, Table 4).

The cells of the corpus luteum of all of these animals were well supported, and the central fibrin clot was invaded by vessels and fibroblasts in all but one animal (no. 3, Table 4; Figure 9). This was also the smallest embryo other than that of the aberrant right specimen (no. 1, Table 4). Its corpus luteum is shown in Figure 11 and is readily distinguishable from the small luteal mass found in the experimental group.

The endometrium had characteristic changes that should allow the histologic diagnosis of early pregnancy. First, the tips of endometrial folds be-

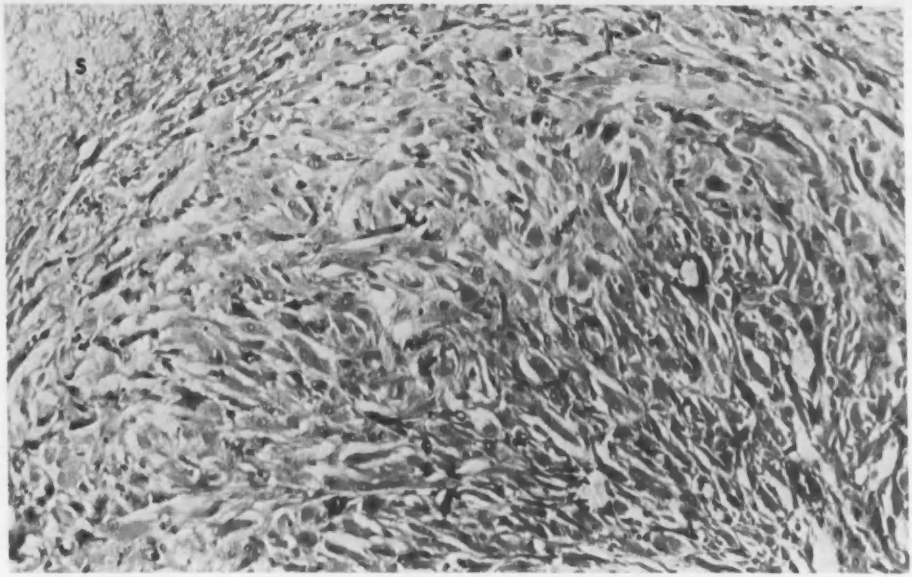

FIGURE 11.—Portion of active corpus luteum of earliest pregnancy with cavity at bottom right and ovarian stroma (S) at top left (no. 3, Table 4; hematoxylin and eosin × 100).

come edematous (Figure 12). At this stage the glands are empty and crowded in the basal portions. Their epithelium lacked mitoses. With advancing pregnancy the edema diminished while secretion accumulated in glands. Most characteristic, however, is the development of a rich capillary network with congestion, most notably in the superficial strata (Figure 13). Despite the presence of significant chronic endometritis in two cases, normally developing early embryos were found.

Group IV, Late Pregnancy

We selected four *S. longirostris* and two *S. attenuata* between 165 and 199 cm in length and embryos of 300-725 mm in length (the *S. attenuata* fetuses were lost at sea) for this comparison (Table 5). All implantations were in the larger left horn but a portion of the membranes traversed into the right horn. The large single corpus luteum of these six specimens was present in the left ovary.

The superficial endometrium was extremely arborized with distended glands into which the villi of the epitheliochorial placenta penetrated, forming an intimately interdigitating connection (Figure 14). The basal endometrium was edematous and glands contained secretion. With advancing gestation the villous arborization increased. The corpus luteum had characteristic appearance (Figure 15). Among the plump, eosinophilic luteal cells streamers of fibrocytes gave the first appear-

TABLE 5.—Group IV: Late pregnant controls. Specimen no. 1-4 *Stenella longirostris*, captured October 1978; no. 5-6 *S. attenuata*, captured July 1976.

Specimen no.	Dolphin length (cm)	Weight of placenta and uterus (g)	Left uterine horn				Right uterine horn				Fetus length (mm)
			Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	
1	197	617	—	—	—	0.60	—	—	—	0.75	300
2	182	703	42	—	—	—	21	—	—	—	429
3	165	700	60	2.69	0.60	0.75	26	5.97	1.49	1.19	557
4	168	982	64	1.79	0.60	0.60	20	—	—	—	725
5	—	730	—	—	—	1.79	12	—	—	0.75	—
6	—	965	—	—	—	2.08	21	—	—	0.60	—

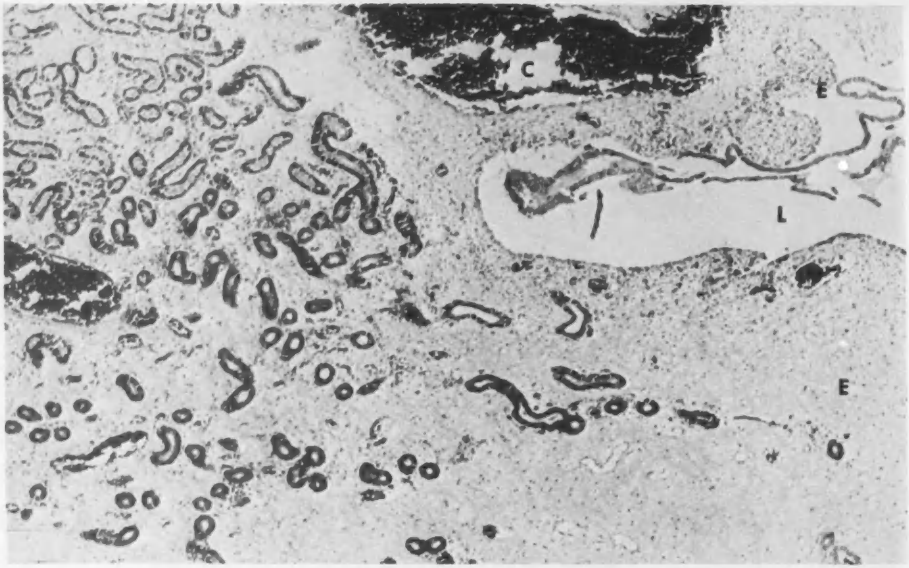

FIGURE 12.—Endometrium of earliest pregnancy (Figures 9, 11; no. 3, Table 4). Uterine lumen (L) at right. Note the marked edema (E) in superficial stroma, congestion (C) and compact arrangement of secretory glands at left (hematoxylin and eosin × 50).

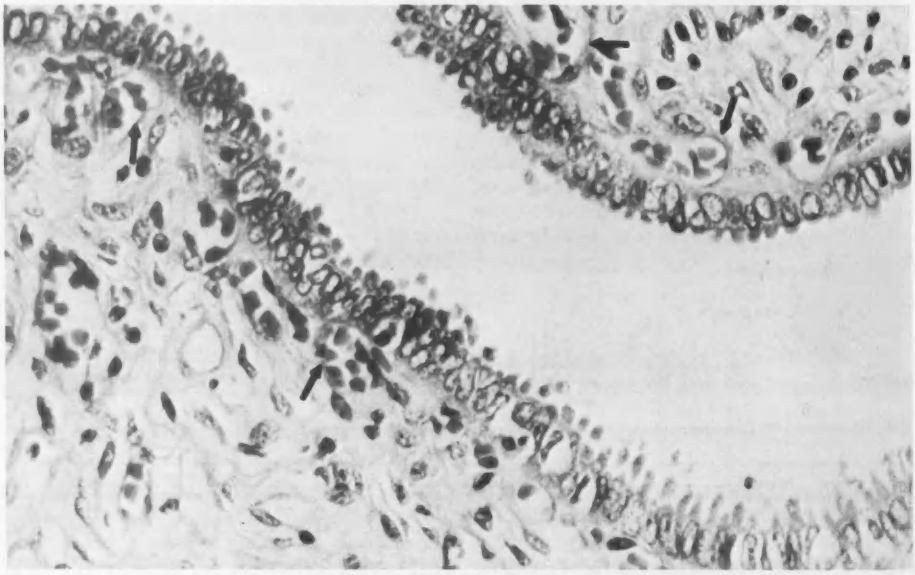

FIGURE 13.—Typical capillary distension (arrows) and neovascularization of endometrial stroma immediately beneath surface endometrial epithelium in early pregnancy (no. 9, Table 4; hematoxylin and eosin × 300).

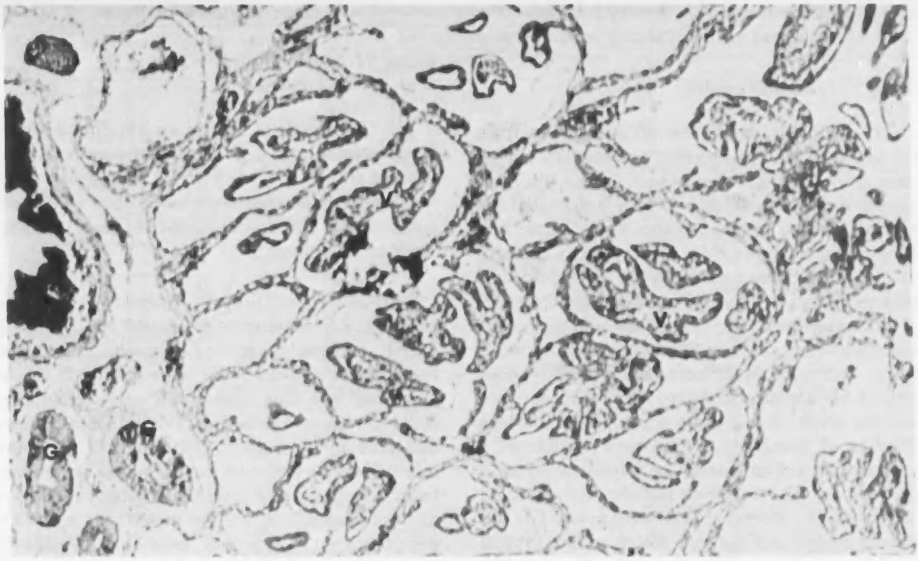

FIGURE 14.—Placental attachment with basal endometrial glands (G) at left and interdigitating villi (V) within distended glandular lumina (no. 2, Table 5; hematoxylin and eosin × 80).

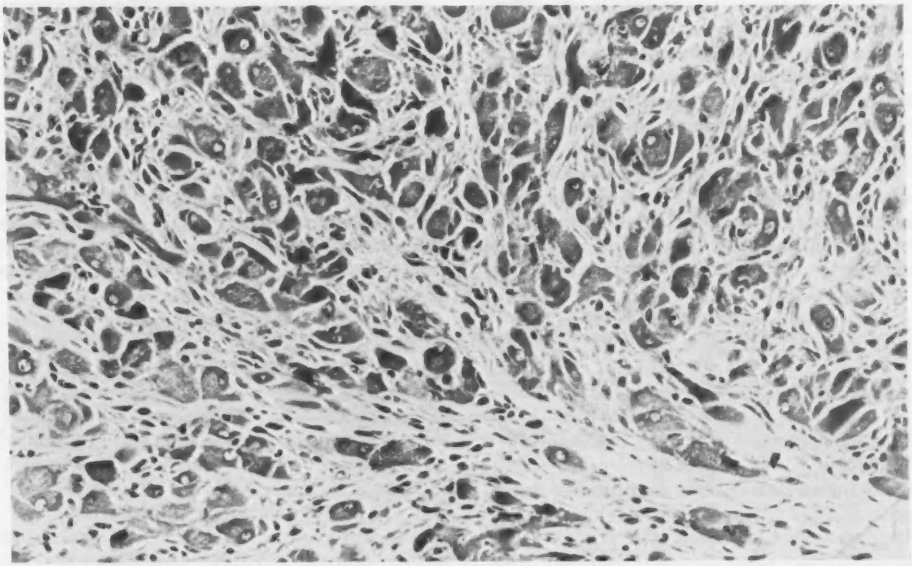

FIGURE 15.—Corpus luteum of uterus shown in Figure 14, the organized cavity is at bottom right. Note well-supported dark luteal cells with fibrocytes in between (hematoxylin and eosin × 150).

ance of degeneration. This connective tissue became less apparent with advancing pregnancy.

Group V, Lactating Females

Six specimens were selected measuring from 167 to 182 cm (*S. longirostris*) and one 202 cm (*S. attenuata*). They had been identified as lactating during dissection at sea. It is a heterogeneous group as judged by uterine size, endometrial histology, and the appearance of the corpora albicantia (Table 6). Some animals must have delivered very recently as evidenced by the marked disparity of uterine horn size, hyperemia, and the recent degenerative changes in the corpus luteum, while others had more equal horns and well-advanced corpora albicantia. No active corpora lutea were present while at least one corpus albicans was found in all specimens. Some corpora albicantia had chronic inflammatory cell infiltration and four ovaries had Graafian follicles maturing at various stages. Stretch marks were present on the uterine serosa and the endometrium had typical involutional changes histologically. Beneath the surface epithelium there was a thin zone of hyalinization in most specimens, while recently delivered animals had prominent, congested vessels in myometrium and endometrium. Some of these had hyalinized walls also. In a majority of endometria a mild chronic inflammatory infiltrate was present; one had acute pyometritis. No mitoses or edema was present, the endometria appeared "resting." Hemosiderin-laden macrophages in endometrium or lower uterine segment were present in three, presumably due to interstitial hemorrhage at recent delivery. Such deposits were found in only one other female (Control Group II) whom we suspect to have delivered recently but who was not recorded as lactating.

Experimental Groups

Group VI, Nonpregnant Animals With Corpus Luteum

The 58 animals of this group were not detected to be pregnant at sea but had a corpus luteum present in one of their ovaries. The group is divided into three subgroups made up of specimens with corpora lutea at different stages of development or involution.

GROUP VIa.—These 28 animals (19 *S. longirostris*; 9 *S. attenuata*) measured 163-191 cm in length, and the group was of special importance because the corpora lutea were judged to be the youngest. For this reason, an early pregnancy could have been overlooked. Two intact uteri were dissected meticulously, including the fallopian tubes. Neither embryos nor placentas were identified in any of the 28 specimens. From the dates of capture (Table 7) it will be noted that most (17) were captured in February, as is also true of early pregnant animals (Table 4). These figures must be interpreted with caution, however, because of different catch sizes on various cruises. The macroscopic findings were not uniform in that uterine weight varied between 90 and 467 g, the horn sizes varied considerably and endometrium was as often congested or mucus-covered as not. Only once was the corpus luteum found in the right ovary.

The histologic appearance of the endometrium correlated neatly with the corpus luteum development and grouping was undertaken accordingly. Those specimens whose corpus luteum had a central fibrin-filled cavity were placed into Group VIa; those whose cavity was replaced by fibrous tissue were adjudged to have ovulated earlier and

TABLE 6.—Group V: Lactating controls. Specimen no. 1-10 *Stenella longirostris*; no. 11 *S. attenuata*.

Specimen no.	Month and year of capture	Dolphin length (cm)	Uterus weight (g)	Left uterine horn				Right uterine horn				Graafian follicle	Corpus albicans
				Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)		
1	Feb. 1976	171	113	14	2.24	0.21	1.64	8	—	0.60	0.90	no	+
2	Feb. 1976	182	112	13	2.29	0.57	2.54	9	2.99	0.66	1.04	+	+
3	Feb. 1976	171	73	11	1.73	0.24	1.64	9	1.19	0.39	1.94	+	+
4	June 1976	171	65	12	1.34	0.30	2.99	11	1.79	0.30	2.09	no	+
5	June 1976	167	126	30	3.88	0.60	1.04	13	3.58	1.64	1.34	+	+
6	Feb. 1976	174	74	15	1.79	0.60	1.49	8	2.24	0.75	0.90	no	+
7	Feb. 1976	175	109	17	2.99	0.24	1.79	8	2.99	0.66	0.90	no	+
8	Feb. 1976	174	198	21	7.91	0.90	2.09	13	6.87	1.13	1.19	no	+
9	Feb. 1976	173	112	12	4.78	1.04	1.04	10	2.09	0.45	1.06	no	+
10	June 1976	173	60	13	1.49	0.75	2.09	12	1.19	0.60	0.75	+	+
11	Sept. 1977	202	550	—	1.64	0.75	2.09	—	1.64	0.60	1.34	no	+
		S. longirostris — Average		3.04	0.56	1.84		2.77	0.72	1.21			

TABLE 7.—Group VIa: Experimental group with early corpora lutea. Specimen no. 1-19 *Stenella longirostris*; no. 20-28 *S. attenuata*.

Specimen no.	Month and year of capture	Dolphin length (cm)	Uterus weight (g)	Left horn of uterus				Right horn of uterus			
				Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)
1	Feb. 1976	184	120	15	5.37	1.72	1.04	19	2.69	1.04	0.75
2	Apr. 1976	182	132	14	4.78	1.49	0.60	14	5.67	1.19	0.75
3	Feb. 1976	171	—	26	4.18	1.49	1.34	16	4.48	1.34	0.60
4	Feb. 1976	176	—	16	4.48	1.94	1.49	14	4.02	1.49	1.34
5	Feb. 1976	173	—	16	2.84	1.19	0.45	18	—	—	0.75
6	Feb. 1976	149	90	15	3.13	0.90	0.96	15	4.18	1.19	1.04
7	Feb. 1976	180	119	25	6.56	0.75	1.34	13	4.18	1.04	1.04
8	Feb. 1976	180	166	20	2.53	0.75	1.04	14	4.18	1.79	0.90
9	Feb. 1976	184	217	25	4.48	1.49	1.19	20	3.28	1.40	0.90
10	Feb. 1976	183	224	18	8.66	1.19	1.34	15	5.97	0.75	1.04
11	Feb. 1976	181	167	16	4.48	1.19	1.94	14	5.97	1.04	0.90
12	Feb. 1976	188	180	18	8.35	0.60	1.79	12	4.78	1.19	0.90
13	Aug. 1976	163	127	16	8.96	0.90	0.90	12	4.48	1.49	1.19
14	Feb. 1976	168	158	21	3.58	1.19	2.69	13	5.07	1.79	1.64
15	Feb. 1976	177	118	20	3.13	0.90	1.49	14	4.18	0.60	0.96
16	Feb. 1976	167	111	17	3.28	2.09	1.04	15	3.58	1.79	0.75
17	Feb. 1976	176	—	22	4.78	0.96	1.34	14	3.58	0.75	1.04
18	Feb. 1976	171	—	14	4.18	1.64	1.19	11	3.28	1.49	1.04
19	Aug. 1976	167	165	22	5.97	2.99	1.49	21	3.88	1.64	0.90
			S. longirostris — Average		4.93	1.33	1.29		4.30	1.28	0.77
20	Oct. 1976	174	190	29	3.88	0.60	1.49	18	3.28	0.84	2.09
21	Feb. 1976	189	192	23	2.98	0.60	1.49	19	2.38	1.19	1.49
22	Aug. 1976	176	390	35	7.46	1.49	1.64	15	—	1.19	1.49
23	Oct. 1975	191	156	25	4.93	1.04	1.34	14	3.58	1.04	1.34
24	Aug. 1976	174	333	26	7.16	1.79	1.94	16	2.99	0.75	1.19
25	May 1976	185	467	27	6.57	1.19	2.39	17	4.48	0.90	1.64
26	Apr. 1976	180	154	18	4.18	1.19	0.90	20	3.28	1.79	1.04
27	June 1977	185	190	12	2.69	0.90	1.19	17	1.79	0.30	0.75
28	June 1977	186	220	13	2.84	0.90	0.90	12	2.39	0.45	1.49
			S. attenuata — Average		4.74	1.01	1.48		3.02	0.94	1.39

placed into Group VIb. Because of the potential insight these specimens give into the dynamics of ovarian/endometrial relationships, these specimens are described in more detail.

When the Graafian follicle has recently ruptured, stromal vessels infiltrate the granulosa layer (Figure 16). The follicular lumen is filled with serous fluid and fibrin but rarely contains blood as in many other species. The corresponding endometrial stroma is edematous, the glands are tubular, lack secretory vacuoles and contain mitoses (Figure 17). When the corpus luteum is better established, the central cavity is more pronounced, capillaries have penetrated the granulosa layer, and, in contrast to its cells in specimens from early pregnancy (Figure 11), they possess less cytoplasm, being less plump (Figure 18). It should again be noted that the cavities rarely contain red blood cells. The endometrial glands at this stage are more crowded, have more coiling, and still possess mitoses, but the earliest appearance of epithelial cytoplasmic vacuoles occurs (Figure 19). The vacuolization appears to commence under the endometrial surface and penetrates slowly throughout the entire thickness of the endometrium (Figure 20). At the same time, fibroblastic infiltration of the corpus luteum cavity has taken place and the luteinized cell wall has folded remarkably. Very few mitoses were found in superficial endometrial cells at this stage and in the final stages before the central corpus luteum cavity has been completely filled in by fibrous tissue, the endometrial stromal edema disappears, to be replaced by coiled secretory glands (Figure 21). No mitoses exist, nor is secretion exuded into the glandular lumina. Such corpora lutea are expected to be associated with early pregnancy particularly because of the conspicuous size of granulosa luteal cells. Since no embryonic sacs were found, it is then also not surprising that the endometrium possesses different histologic features from those whose comparable corpora lutea were associated with early pregnancy (Figures 11-13). Perhaps this climaxes endometrial development before regression of corpus luteum occurs.

One of these specimens from an October catch (no. 20, Table 6) had a fresh corpus luteum with fibrin-filled cavity and unusual endometrium. The stroma beneath the surface epithelium had the typical hyalinization of the post partum state, yet, early secretory endometrium was found in deeper layers (Figure 22). Moreover, hemosiderin pigment was found. It would appear that this was the first and infertile ovulation after a recently past pregnancy which is further supported by the

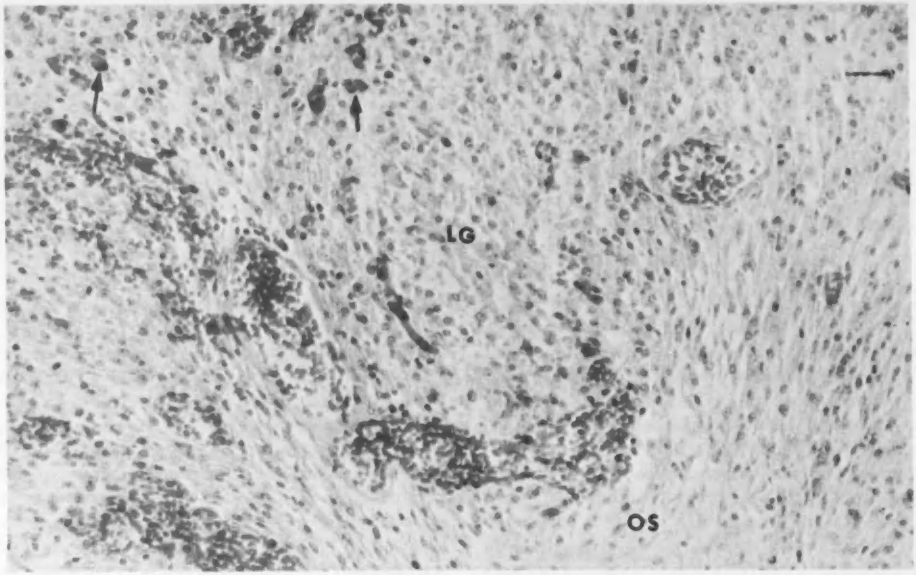

FIGURE 16.—Very fresh corpus luteum with focal hemorrhages (left), luteinized granulosa cells (LG) infiltrated by capillaries (arrows) sprouting from the ovarian stroma (OS) (no. 18, Table 7; hematoxylin and eosin × 400).

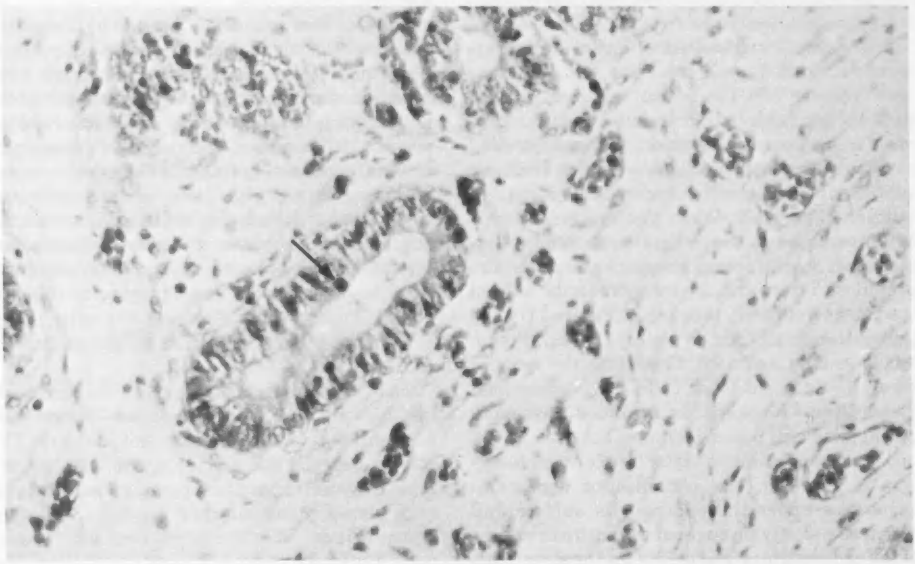

FIGURE 17.—Endometrium of specimen in Figure 16 with glandular mitosis at arrow. Note stromal edema (hematoxylin and eosin × 400).

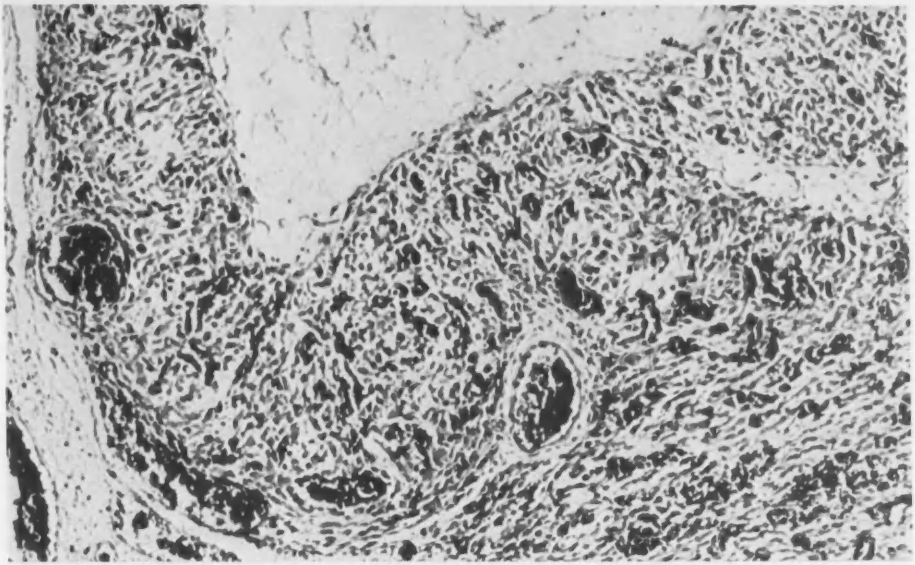

FIGURE 18.—Young corpus luteum in nonpregnant animal. Note central cavity (top) is filled with fibrin and granulosa layer is penetrated by capillaries (black). Size of granulosa lutein cells is much smaller than in Figure 11, an early pregnant specimen (no. 3, Table 7; hematoxylin and eosin × 100).

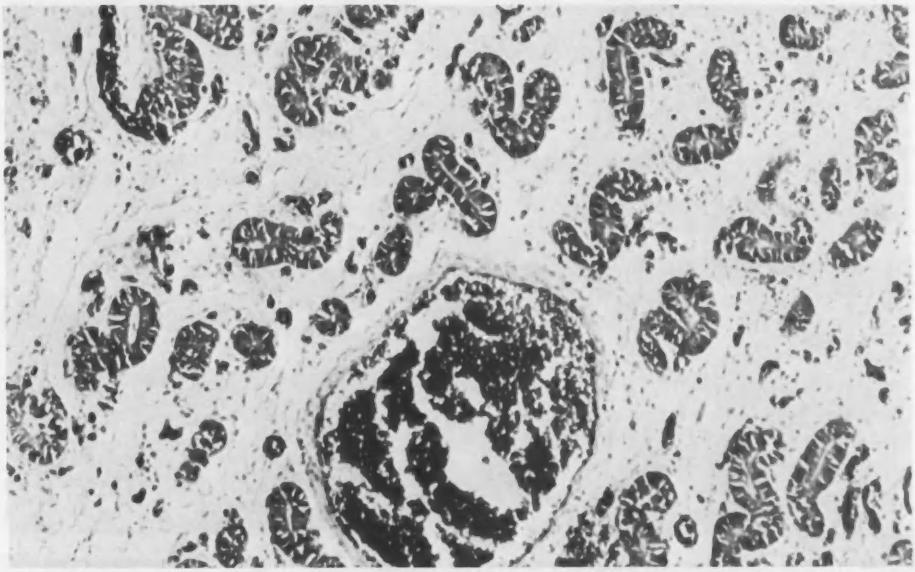

FIGURE 19.—Endometrium of same specimen as Figure 18 to show increased glandular coiling and earliest appearance of light cytoplasmic vacuoles in dark epithelial cells (hematoxylin and eosin × 100).

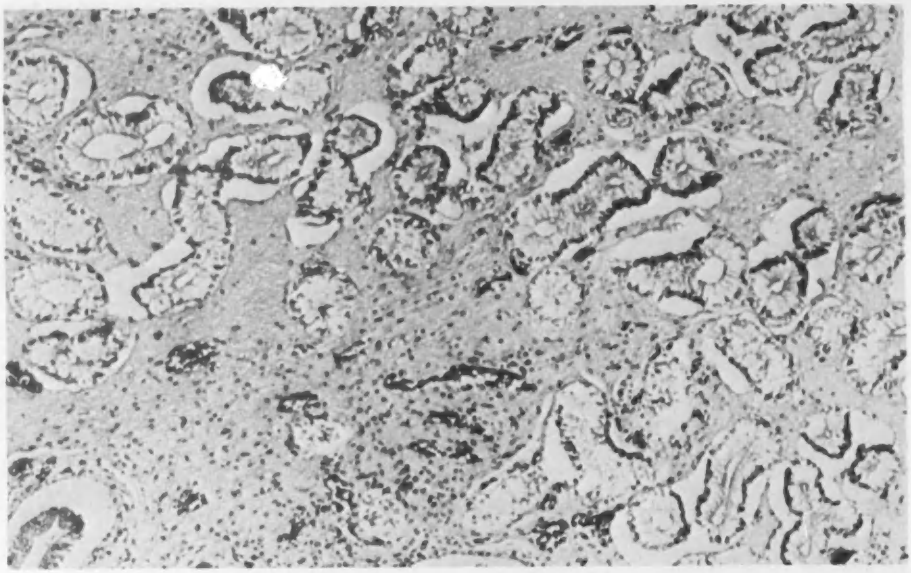

FIGURE 20.—Endometrium of nonpregnant *Stenella longirostris* with well-established corpus luteum, to show secretory vacuoles in endometrial glands as well as stromal edema (no. 10, Table 7; hematoxylin and eosin × 100).

FIGURE 21.—Final stages of secretory change in endometrium of nonpregnant *Stenella longirostris* with advanced corpus luteum. Crowding of secretory glands occurs in stroma that has now lost its edema. No secretion in lumen. Endometrial cavity at right (no. 16, Table 7; hematoxylin and eosin × 100).

FIGURE 22.—Endometrium of presumably delivered *Stenella attenuata* whose ovary had a fresh corpus luteum. Endometrial cavity top left, hyalinized stroma (HyS) beneath surface epithelium and secretory glands (SG) beneath this layer (no. 20, Table 7; hematoxylin and eosin × 100).

marked discrepancy of the uterine horns (29 cm left; 18 cm right).

GROUP VIb.—These 15 animals (11 *S. longirostris*; 4 *S. attenuata*) were found to be nonpregnant but had well-established corpora lutea with completely organized cavities, the luteal cells appeared well supported (Table 8). Their lengths varied from 169 to 198 cm and uterine weights were between 110 and 580 g. One of these specimens had not been opened, was carefully dissected by us, and found to be nonpregnant. Again, most (12) were from February catches, many uteri had stretch marks from former pregnancy, and in two ovaries the corpus luteum was found on the right.

The secretory endometrium of almost all these

TABLE 8.—Group VIb: Experimental group with well-supported corpora lutea. Specimen no. 1-11 *Stenella longirostris*; no. 12-15 *S. attenuata*.

Specimen no.	Month and year of capture	Dolphin length (cm)	Uterus weight (g)	Left uterine horn				Right uterine horn			
				Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)
1	Feb. 1976	191	281	21	5.97	1.19	0.66	18	5.07	1.64	0.60
2	Feb. 1976	169	—	17	2.23	1.64	0.90	14	1.94	1.19	0.84
3	Feb. 1976	180	—	19	4.18	1.04	0.75	13	3.28	1.04	0.75
4	Feb. 1976	184	142	18	7.16	0.84	1.49	16	6.57	1.49	1.79
5	Feb. 1976	180	149	22	5.67	0.90	1.19	16	4.33	1.04	1.19
6	May 1976	178	268	24	4.48	1.04	1.94	19	2.84	0.75	1.34
7	Feb. 1976	180	194	20	3.58	1.34	1.34	16	3.73	1.94	0.90
8	Feb. 1976	178	227	21	4.18	0.75	1.19	13	3.28	1.19	1.04
9	Feb. 1976	181	148	16	3.58	1.19	1.34	11	3.28	1.19	1.19
10	Feb. 1976	170	117	18	4.48	1.04	1.04	15	3.88	1.04	1.49
11	Feb. 1976	181	166	21	1.79	0.90	1.19	12	2.99	1.04	1.04
			S. longirostris — Average		4.30	1.08	1.18		3.74	1.23	1.11
12	Feb. 1976	193	250	24	5.67	2.09	1.34	23	2.84	1.19	0.90
13	Feb. 1976	184	110	11	3.28	0.90	1.04	10	4.18	0.90	0.84
14	June 1977	185	240	22	2.39	1.19	1.79	17	1.79	0.60	1.88
15	Nov. 1975	198	580	37	5.67	1.49	2.09	21	6.87	1.49	2.39
			S. attenuata — Average		4.25	1.42	1.57		3.92	1.05	1.50

specimens showed great similarity with those shown in Figures 20 and 21. The amount of edema varied slightly and so did the glandular vacuolization. No secretion was found within the glands although frequently there was thick mucus covering the endometrial surface on gross examination. The luteal cells were supported, not degenerated but less plump than in early pregnancy. The only difference was the complete fibrosis of the central cavity, probably insufficient findings for a meaningful separation of some specimens from the previous group VIa. Of course, no capillary proliferation of the superficial endometrium, so typical of pregnancy was evident.

One specimen is probably misclassified (no. 15, Table 8). Not only is this the largest uterus (580 g) with pronounced stretch marks (Figure 23) but also it exhibits a differing histologic appearance of the endometrium (Figure 24). This shows acute endometritis in a mucosa which otherwise had all of the characteristics of pregnancy. The corpus luteum was well supported with large plump cells. In all likelihood this *S. attenuata* had very recently delivered. This is from a November catch and it is impossible to determine whether this represented a full-term pregnancy since Perrin et al. (1976) showed that calving does occur in this species in the winter, although less commonly. It may well be that this inflammatory exudate in the superficial endometrial regions represents the normal immediately post partum event. This would explain the persistence of an active corpus

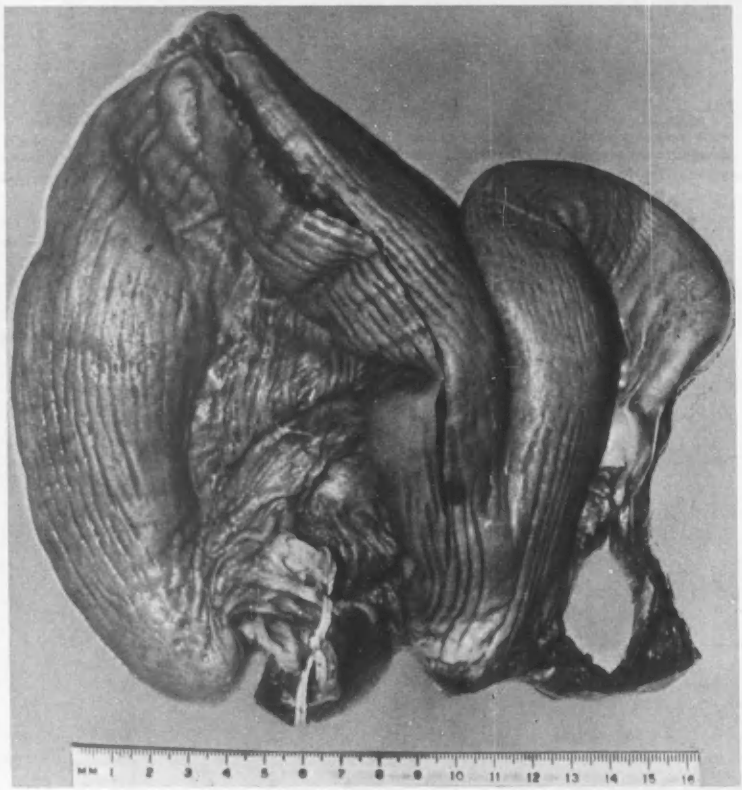

FIGURE 23.—Uterus of recently delivered *Stenella attenuata*, no. 15, Table 8. Note stretch marks of left horn, congestion and disparate size of horns.

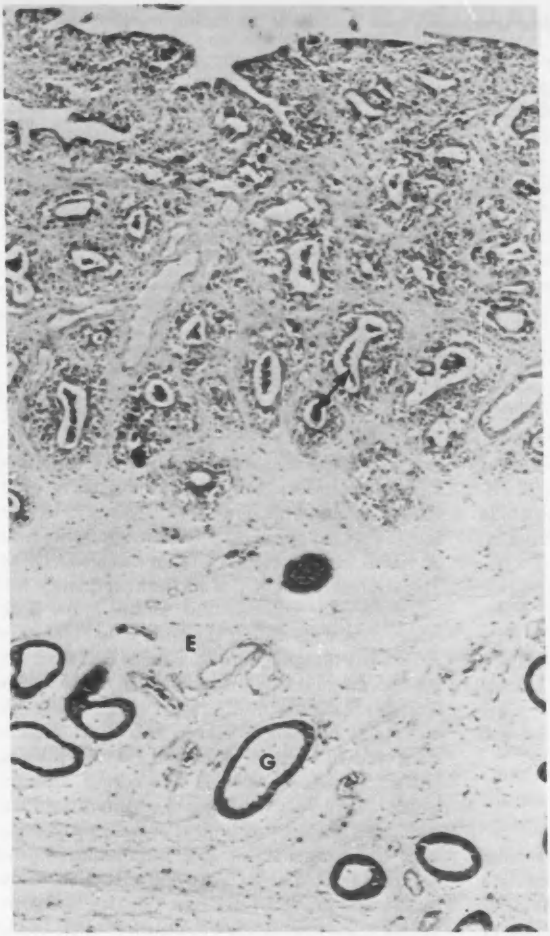

FIGURE 24.—Endometrium of uterus in Figure 23. The marked stromal edema (E) and distended glands (G) of basal endometrium are typical of late pregnancy. The superficial endometrium is infiltrated by polymorphonuclear leukocytes that exude into the glandular lumina (arrow). No surface stromal hyalinization has yet taken place. The former interdigitation of placental villi with surface endometrium can be imagined from the irregularities the surface presents (hematoxylin and eosin × 100).

luteum, presumably destined to involute shortly.

GROUP VIc.—This composes 15 animals (8 *S. longirostris*; 7 *S. attenuata*) measuring 162-193 cm whose features are listed in Table 9. These nonpregnant dolphins possessed histologically regressing corpora lutea. Eight animals in fact had corpora albicantia and were probably misclassified by the gross observations because the corpus luteum in each case was recently involuted, had still some vascularization and microscopic inflammation. Similarly, the endometria in these specimens usually had inflammation and hyalinization and were most likely recently delivered. This is further supported by the disparity in uterine horns. These animals were not listed as lactating either because this feature had been overlooked or perhaps the calves had died or were aborted. This material does not allow this differentiation.

Six of the remaining seven animals had corpora lutea with histologic signs of early degeneration. Two had late secretory endometrium and this would likely to have involuted upon further regression of the corpus luteum since pregnancy did not occur. Two animals had marked chronic en-

TABLE 9.—Group VIc: Experimental group with degenerating corpora lutea. Specimen no. 1-8 *Stenella longirostris*; no. 9-15 *S. attenuata*.

Specimen no.	Month and year of capture	Dolphin length (cm)	Uterus weight (g)	Left horn of uterus				Right horn of uterus			
				Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)
1	Sept. 1976	162	250	32	5.22	1.19	2.24	15	3.88	1.19	1.64
2	Feb. 1976	175	252	25	10.14	2.09	1.19	12	—	—	1.04
3	May 1976	183	273	25	4.93	1.04	1.19	15	3.88	1.19	1.04
4	Feb. 1976	179	—	23	4.78	0.90	1.19	14	4.48	1.94	1.34
5	Feb. 1976	185	—	21	2.00	0.90	0.90	16	1.19	1.04	0.75
6	Feb. 1976	186	—	22	2.24	0.75	0.90	16	1.04	0.45	0.90
7	Feb. 1976	186	291	25	5.37	1.19	1.34	14	3.58	0.90	1.04
8	Mar. 1976	189	197	17	5.37	1.19	1.64	13	3.28	1.04	1.04
			S. longirostris — Average		5.02	1.16	1.32		3.05	1.11	1.10
9	Aug. 1976	172	145	—	1.64	0.45	0.90	—	2.09	0.60	0.60
10	Feb. 1976	180	122	18	5.79	1.34	1.64	15	6.57	1.19	1.04
11	Feb. 1976	185	—	23	3.13	0.90	1.34	18	2.39	0.60	1.04
12	May 1976	191	205	18	4.18	0.75	1.79	18	2.39	0.60	1.79
13	June 1976	193	375	22	8.80	1.94	2.09	15	6.42	1.79	1.79
14	Aug. 1976	179	356	30	6.57	1.04	1.79	18	5.07	0.75	0.90
15	Apr. 1976	185	305	25	4.18	0.90	1.49	13	3.28	0.90	1.64
			S. attenuata — Average		4.90	1.05	1.60		4.03	0.92	1.26

dometritis. Two others had marked endometrial stromal edema in addition to having horns of different lengths. The possibility of abortion exists in these animals but this cannot be proven. Finally, one animal of this heterogeneous group (no. 12, Table 9) had equal uterine horns (18 cm) and possessed corpora albicantia in addition to a degenerating right-sided corpus luteum. The endometrium with hyalinization and capillary development suggested recent pregnancy but because of the size of the uterus (205 g) it appears likely that a recent right-sided pregnancy had ended in abortion.

DISCUSSION

Although conclusive proof is lacking, the results support the notion that dolphins may ovulate spontaneously, at least at times. Control material of different reproductive phases (96 specimens) of the two species of dolphin investigated, the eastern spinner dolphin, *S. longirostris*, and the spotted dolphin, *S. attenuata*, provided a life history of the macroscopic and microscopic events in the uteri and ovaries of these species for the first time. The principal findings were the following: In three immature animals neither corpora lutea nor corpora albicantia were present in the ovaries but Graafian follicles were forming. The endometrium had tubular glands. Six mature animals without corpus luteum all were found to have one or more corpus albicans, the horns were disparate in size, five had stretch marks as an excellent sign of former pregnancy, in most the inactive endometrium possessed inflammatory cells, hyalinization, had hemosiderin macrophages as indications of former pregnancy. Eleven of twelve early pregnant animals with embryonic sizes of 1-53 mm had the pregnancy in the left horn; one in the right on which side the corpus luteum was also located. The endometrium of the earliest pregnancy had characteristic changes that should allow pregnancy diagnosis even if the embryo is overlooked or lost. Six late pregnant specimens had their corpus luteum in the left ovary, typical epitheliochorial implantation and again characteristic endometrial histology. Eleven lactating females were studied, none of which had a corpus luteum, but all possessed at least one corpus albicans which was in various stages of degeneration. The endometrium showed typical regressive changes with hyalinization, chronic inflammation, and hemosiderin. These features will also allow categorization of uteri from females with unknown reproductive state in future studies. Of the 58 animals with macroscopically diagnosed corpora lutea and no detectable pregnancy, only 43 in fact had an active corpus luteum, the remaining 15 specimens had corpora albicantia in various stages of regression. Three corpora lutea were on the right, the remaining 40 were on the left, confirming the usual finding of Cetacea that the left side predominates in reproduction. When a correlation was sought between the development of the corpus luteum and endometrial changes a well-delineated cycle of proliferation and edema to secretory stages emerged. No changes indicative of early pregnancy were seen and three intact uteri contained no embryos. Thus, clearly, ovulation does occur without pregnancy ensuing. In three

specimens the findings are consistent with abortion, two had marked endometritis. These latter findings are summarized in Table 10.

TABLE 10.—Group VI: Summary of experimental, nonpregnant animals; 38 *Stenella longirostris*, 20 *S. attenuata*.

S. longirostris:		
19	(50%)	Fresh corpus luteum
11	(29%)	Well-established corpus luteum
8	(21%)	Degenerating corpus luteum—wrong gross diagnosis (2 endometritis; 2 unimplanted abortion?)
S. attenuata:		
9	(45%)	Fresh corpus luteum
3	(15%)	Well-established corpus luteum
1	(5%)	Misclassified, recently delivered
7	(35%)	Degenerating corpus luteum—wrong gross diagnosis (1 recent abortion?)

The findings of Perrin et al. (1976, 1977) indicate that over 90% of female genital tracts of *S. longirostris* and *S. attenuata* contain a corpus luteum because of their pregnancy. The possibility that abortions of implanted pregnancies occur frequently can be ruled out from the histologic appearance of the endometria in the majority of the specimens from the experimental group. Early embryonic death remains a possibility although no evidence can be adduced for this. The present study provides strong evidence that spontaneous ovulation may occur in these species, at least that the presence of a corpus luteum is not indicative of pregnancy. Moreover, recent and as yet unpublished results from our laboratory (J. Sawyer) have identified hormonally the occurrence of spontaneous ovulation in a *Delphinus delphis* female that was kept in isolation. Evidence for regression of corpora lutea in nonfertile cycles was also found in our experimental group. It is possible then that either ovulation is induced in a majority of cycles or that a majority of dolphins become pregnant when ovulating. In either case, it is not likely that a count of corpora albicantia in dolphin ovaries accurately reflects the number of past pregnancies. We were unable to differentiate with certainty between the histologic appearance of a corpus luteum of early pregnancy and one from nonpregnant animals and cannot accept the alleged feasibility of the diagnosis of pregnancy from the histology of only a corpus luteum. The endometrial histology is a better guide. Whereas accessory corpora lutea have been found in other odontocetes (Brodie 1972), no such structures were encountered in the genital tracts of these two *Stenella* species.

It would be useful to know from aquaria with accurate historical information and pathologic study at death whether older females that have been kept in isolation since youth possess corpora albicantia. Inasmuch as the question of artificial insemination of exhibited animals has been raised in the past (Hill and Gilmartin 1977) it can be concluded that it would appear feasible without the need of superovulation.

From a practical standpoint it is suggested that the following points be considered in future studies. First, it would have been helpful to have had a histologic sample of mammary gland and vagina in all specimens to enhance histologic correlations. Moreover, inasmuch as the hormonal cycle of *D. delphis* is now being defined by modern endocrine techniques undertaken by sequential sampling of captive specimens it may be useful for future studies to save, for endocrine analysis, an aliquot of frozen serum. Potentially, such a study would clarify the status of equivocal corpora lutea. At the same time storage of fetal serum would allow insight into the fetal endocrine behavior which is known to differ so markedly between species. Perhaps such comparative studies will ultimately give additional insight into the phylogenetic descendency of Cetacea.

This study extends the sparse literature that exists on the morphology of the female reproductive organs. In general, the endometrial cycle is similar to that illustrated schematically for several whales (Slijper 1966) and for *Globiocephala melaena* (Harrison 1949). In this latter species Harrison (1949) also described the small superficial anastomosing vessels beneath the uterine epithelium and, in three recently ovulated specimens, he was unable to identify products of conception. In a later contribution, Harrison et al. (1969) suggested that while ovulation in *Tursiops truncatus* appears to be of a reflex nature, that of *S. graffmani* and *Lagenorhynchus obliquidens* may be spontaneous as in *G. melaena*. Our own findings cited above suggest, however, that in *D. delphis* spontaneous ovulation occurs and one wonders whether this then may not be the rule in Cetacea. A resolution can come only from longitudinal endocrine studies of isolated females from different species. Finally, as was the case in most other studies of the morphology of Cetacean reproductive organs, we observed no significant pathologic features in these specimens other than the endometritis described and occasional parametrial parasitic granulomata.

ACKNOWLEDGMENTS

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NOTES

A LARGE, OPENING-CLOSING MIDWATER TRAWL FOR SAMPLING OCEANIC NEKTON, AND COMPARISON OF CATCHES WITH AN ISAACS-KIDD MIDWATER TRAWL

Avoidance of nets by agile micronekton and nekton is one of the major problems with small midwater trawls routinely used for oceanic sampling by oceanographers and marine biologists (e.g., Harrisson 1967; Pearcy 1975; Roper 1977). A major advantage of small trawls is that they can be equipped with opening-closing devices so that samples can be ascribed to discrete depths. This capability is especially important for sampling deep water where densities of animals are low. An opening-closing rectangular midwater trawl with a mouth area of about 25 m^2 is the largest opening-closing net described (Baker et al. 1973). Another important advantage of small nets is that they can be used from most oceanographic vessels.

Large, commercial-size midwater trawls used to sample oceanic micronekton (Berry and Perkins 1966; Harrisson 1967; Taylor 1968; Clarke 1973, 1974; Krefft 1974; Roper 1977) are usually not evaded as successfully by nektonic animals. Big nets which filter large volumes of water have the added advantage of catching enough animals to characterize species and size composition from sparsely populated waters. However, these large nets lack opening-closing capability, and most oceanographic research vessels are unable to handle large nets, otter doors, and bridles (Pearcy 1975).

This paper describes a 50 m^2 pelagic trawl especially designed for use with an opening-closing cod end, attempts to evaluate its performance, and compares its catches of mesopelagic fishes and cephalopods with those from a 5.4 m^2 Isaacs-Kidd midwater trawl.

Midwater Trawl Description and Operation

The midwater or pelagic trawl was designed by G. Loverich, Nor'Eastern Trawl Systems, Inc.,[1] Bainbridge Island, Wash., for sampling mesopelagic fishes and cephalopods in conjunction with a 1 m^2 five-net opening-closing device which is attached to the cod end of the trawl (Figure 1). The body of the trawl is lined throughout with 19 mm (¾ in) stretch mesh. The net is 42 m long and was constructed with a gradual taper from mouth to cod end in order to provide a large netting area for filtration in order to reduce the water velocity through the meshes, stagnation and hang-up of animals on the netting, and extrusion of animals through the netting. The wings of the trawl are made of large mesh (292 mm). It was assumed that micronekton (fishes, squids, and shrimps up to 200 mm in length) escape or pass through this large mesh rather than lead into the trawl body, giving an effective diameter of the net for micronekton equivalent to the small mesh body of the trawl. Unfortunately data do not exist to evaluate herding or leading of oceanic micronekton by the wings of trawls.

The trawl has six seams with four identical panels for the top and bottom (wing, body, and intermediate) two identical side (wing, body, and intermediate) panels, and four cod end panels (Figure 2). The meshes were hung at 29.3% in both directions to allow formation of square openings and laced to make six seamlines. Two riblines are located along the middle of the side panels and extend to the opening-closing device.

A 1 m^2 Multiple Plankton Sampler (MPS) with five separate nets, each 4.6 m long (see Pearcy et al. 1977 for details), was used as an opening-closing cod end device on the trawl. The levers for release of the five nets of the sampler are actuated by a modular timer which employed a crystal oscillator and a binary series of counters for selection of release times (Evans 1975). The timer is mounted on the MPS, started as the trawl is launched, and is set to give the trawl time to stabilize at a selected towing depth before net 1 is released (usually 30-60 min). Thus the first net fishes obliquely from the surface to the fishing depth of net 2. The four remaining nets (nets 2-5) all fish the same amount of time on a given tow (usually 40 min), either at the same depth (horizontal series) or at different depths (vertically stratified series).

The footrope and headrope are each 28.6 m of 16

[1]Reference to trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

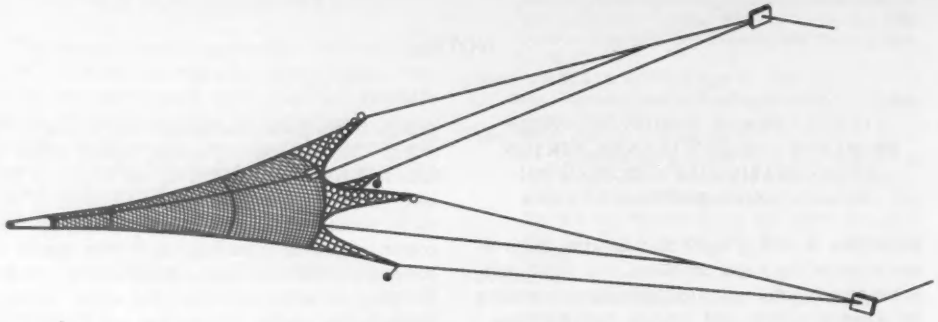

FIGURE 1.—Sketch of the pelagic trawl in operation.

mm poly-Dacron rope. The wings are of #60 thread, the body of #3 thread, the intermediate of #4 thread, and the cod end of #6 thread. Nineteen 25.4 cm (diameter) aluminum floats (good to 1,000 m) are attached to the headrope. Galvanized chain is attached to the footrope and one 23 kg lead ball is attached to the tip of each of the bottom wings. The bridles to the bottom wings are 55 m long; bridles to the upper wing are 36 m long, and the middle bridle is 47 m long (Figure 1).

The trawl was designed to be towed with 1.5-1.8 × 2.4-2.7 m (5 × 8 ft or 6 × 9 ft) otter doors. A scale model of the trawl was first constructed and tested in a tank to test its design and performance.

Observations were made on the trawl by divers during trials in Puget Sound using 1.8 × 2.7 m doors and towing speeds of 1.0 to 1.6 m/s at depths of about 12 m. The towing characteristics of the net were observed and the number of floats needed to provide neutral buoyancy to the cod end opening-closing device was determined by trial. At a towing speed of 1.6 m/s the vertical opening of the mouth was measured to be about 8 m and the body of the trawl was observed to be nearly circular and about 8 m in diameter, providing an estimate of about 50 m^2 for the cross-sectional area of the fine mesh netting of the trawl body.

The depth that each net fished was determined from the depth-modulated signal from an acoustical pinger mounted on the headrope of the trawl, a hydrophone towed from the vessel, and a graphic recorder. An EG&G pinger was used initially but was replaced with an Institute of Oceanographic Sciences (IOS) 0-683 m (0-100 atmospheres pressure) acoustical net monitoring system (Baker et al. 1973) with an overall accuracy of 0.1% of the full depth range.

Methods

A timer-actuated ejection device was used as a method to provide some information on the flushing rate through the body of the trawl. This device, similar to the one described by Pearcy et al. (1977), has a modular timer (Evans 1975) to release the contents of two 1.3 l chambers. It was hung from the headrope inside the trawl mouth and its contents were ejected against the 19 mm mesh. Preserved juvenile salmon (10-20 cm total length) were released into the net at intervals of 5, 10, 15, or 25 min before closure of net 1 and opening of net 2.

The pelagic trawl-MPS combination was used on three chartered trawlers off Oregon. All vessels had net reels and used double-warp towing. A boom was used to launch and recover the MPS during 1975 and 1976 cruises. The vessel chartered in 1977 had a stern ramp, which greatly facilitated use of the pelagic trawl. Twelve tows were made in 1975 to test the monitoring equipment and to evaluate flushing of the net. Eight tows were made in 1976 and 10 in 1977. All tows were 110-130 km off the central Oregon coast; 18 of these tows provided the data for comparison of pelagic trawls and Isaacs-Kidd midwater trawls (IKMT's) (Table 1).

Tows were also made with a 5.4 m^2 IKMT with 10 mm stretch mesh and a 1 m^2 MPS opening-closing device (Pearcy et al. 1977) at 1.5-2.0 m/s at a similar location and within 10 days after each of three cruises that used the pelagic trawl (Table 1). Volume of water entering the IKMT was monitored with a modified TSK flowmeter on all tows. One of the purposes of these IKMT tows was to enable comparisons of the catches by the two different types of nets.

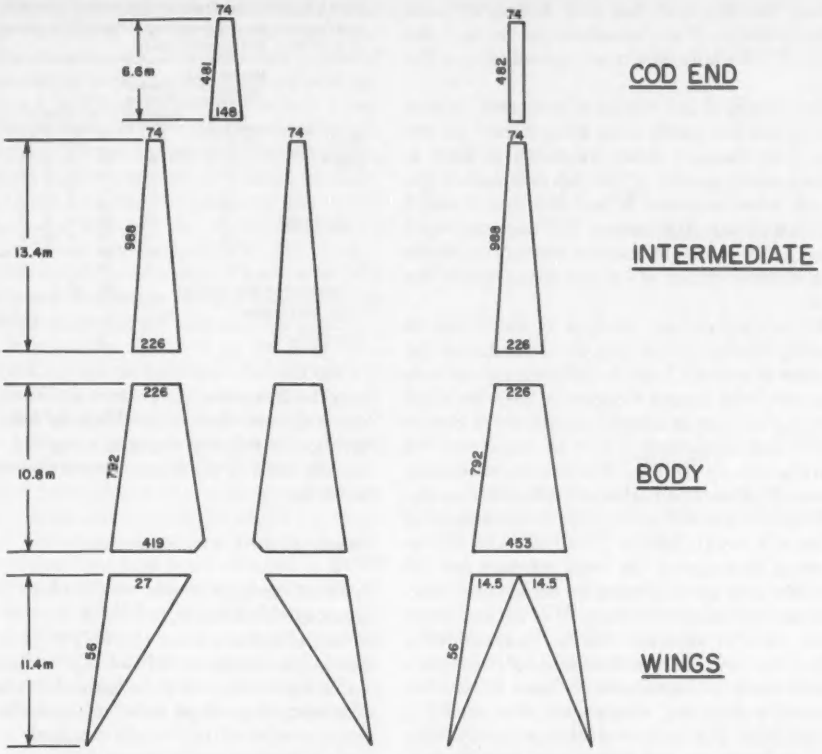

FIGURE 2.—Net plans for the pelagic trawl. Numbers on the net panels indicate number of meshes along the margins.

Collections were preserved in 10% Formalin at sea. In several instances large catches (>35 l) of the pelagic trawl were subsampled, but at least 14 l of the catch of each of the nets for discrete depths were preserved. Fishes and cephalopods were identified and measured [standard length (SL) of fishes and dorsal mantle length (DML) of squids].

TABLE 1.—Summary of pelagic trawl (PT) and Isaacs-Kidd midwater trawl (IKMT) tows made on the three "paired" cruises off Oregon.

Net	Dates	Vessel	No. Tows	Depth (m)	Time
	1975:				
PT	23 Sept.	*Betty-A*	1	340-360	Day
IKMT	12-16 Sept.	*Yaquina*	5	334-362	Day
	1976:				
PT	19-22 July	*Pacific Raider*	8	0-500	Day-night
IKMT	8-13 July	*Wecoma*	11	0-465	Day-night
	1977:				
PT	30 July-2 Aug.	*Excalibur*	9	185-365	Day-night
IKMT	8-10 Aug.	*Wecoma*	5	187-350	Day-night

Results

Flushing of the Pelagic Trawl

In Puget Sound, divers observed that dead salmon smolts released in the mouth of the trawl were never stuck against the netting in the forward part of the trawl where the meshes were taut from water pressure. Occasionally fish stalled against the mesh in the aft section of net where netting was less rigid, but these fish were easily dislodged and tumbled toward the cod end. Because live fishes usually swim away from the netting when inside a trawl, it seems unlikely that live, active fish would be pinned against the netting (G. Loverich[2]). Obviously, dead, preserved fish do not

[2]G. Loverich, Nor'Eastern Trawl Systems, Inc., Bainbridge Island, WA 98110, pers. commun. January 1979.

behave like live ones, but they do provide some information on flow characteristics through the net and how easily objects are pinned against the mesh.

The results of the release of preserved salmon smolts into the mouth of the pelagic trawl on two cruises in the open ocean are shown in Table 2. Ninety-seven percent of the fish released in the mouth were recovered in cod end nets 1 and 2 within 5-25 min after release: 82% were recovered in net 1. These data indicate an average residence time of preserved fish of <10 min in the body of the trawl.

If live animals were delayed by 10-120 min in passing through the net into the cod end, then the number of animals found in different cod end nets may vary, with largest numbers in latter nets and fewest in the first or second net as found by Foxton (1970) and Donaldson (1975) in other cod end opening-closing devices. Coefficients of concordance, W, (Tate and Clelland 1957) were not significant ($P>0.2$) for rank order of abundance of fishes (12 tows), squids (10 tows), and *Stenobrachius leucopsarus*, the most common fish (10 tows) for nets 2-5 that sampled equal time intervals and also caught at least 10 of each of these three types of animals. Similar nonparametric tests of the rank order of abundance of 15 common species were not significant for nets 2-5 of nine tows with same net, where each net fished 2 h (Willis 1979). This lack of correlation of catch with net number provides no evidence for delay or stagnation of animals in the net over time periods of 10 min to 6 h. Characteristic species compositions or size-frequency distributions from specific depths (Willis and Pearcy[3]) also indicate that cod end catches are predominantly from the depths fished.

Entanglement or hang-up of fishes and cephalopods in the meshes of the trawl appeared to be restricted to a few types. Fishes such as the stomiatoid, *Tactostoma macropus*, were occasionally found hanging on the meshes of the trawl body by their teeth. Soft-bodied cephalopods, such as *Chiroteuthis calyx* and *Vampyroteuthis infernalis*, were sometimes entangled in the mesh. The number of animals hung on the net after a tow was always a small fraction of those in the cod ends. These entangled animals that are retained in the net from one tow are probably washed-down into the first net of the next trawl. Since this first net is the one that fishes obliquely from the surface to the selected depth of sampling, it is not usually used in studying vertical distribution of animals.

TABLE 2.—Results of release of preserved salmon from the ejection device in front of the pelagic trawl. All tows were horizontal at 2.5-3.0 kn. ND means no data.

Vessel	Minutes that ejection device was set to go off before closure of net 1	Interval between closure of nets 2-5 (min)	No. of fish in net: 1	2	3	4	5	No. recovered/no. used
Betty-A	10	15	35	0	0	(1)	(1)	ND
	10	15	35	0	0	0	(1)	ND
	10	15	30	3	0	0	0	ND
	25	20	36	0	0	0	0	ND
Pacific Raider	5	40	30	24	1	4	2	61/65
	10	40	[2]0	[2]34	[2]2	[2]0	[2]7	43/60
	10	40	33	25	0	0	0	58/60
	15	40	49	1	0	0	2	52/59
Percent recovered in each net			82	15	1	1	1	

[1] Net failed to close.
[2] Cod end of trawl was twisted. This trawl was excluded from percentage calculations.

Pelagic Trawl-IKMT Comparisons

The 17 pelagic trawls caught almost twice as many species of fishes, and about the same number of cephalopod species as the 16 IKMT's during the two major cruises in 1976 and 1977. These differences are mainly due to the large volumes of water filtered by the pelagic trawl and consequently the large number of individuals captured.

One of the most significant differences between the catches was the presence of some fish species in the pelagic trawl and their complete absence in the IKMT catches (number caught-vessel, where PR = *Pacific Raider* and EX = *Excalibur*): *Aphanophus carbo* (3-PR), *Merluccius productus* (3-PR), *Idiacanthus antrostomus* (23-PR), *Aristostomias scintillans* (24-PR, 6-EX), Macrouridae (5-PR), *Lestidium ringens* (37-EX), *Nansenia candida* (22-EX), *Symbolophorus californiensis* (5-EX). In over 2,000 (2, 2.5, and 3 m mouth opening) IKMT tows made off Oregon since 1961, we have never before captured *Aphanophus carbo* or *M. productus* in oceanic waters. These fishes were large (436-570 mm) and presumably always avoid IKMT's.

Length-Frequency Comparisons

Significant differences [$P<0.5$, Kolmogorov-Smirov (K-S) two sample comparisons (Tate and Clelland 1957)] were found in the size-frequency

[3] Willis, J. M., and W. G. Pearcy. Spatial and temporal variation in the population size structure of three lanternfishes (Myctophidae) off Oregon. Unpubl. manuscr.

distributions of four common species (where $n>50$ for fishes for each of the two nets, and $n>20$ for squid) for: *Stenobranchius leucopsarus* in two of the three comparisons, *Diaphus theta* in one of two comparisons, and *Tarletonbeania crenularis* in two of two comparisons. In all instances where length distributions differed, the pelagic trawl caught an appreciably higher percentage of large animals. Even though the one K-S test for the squid *Gonatus pyros* was not significant (because of small numbers caught in the IKMT), 15% of numbers of this squid from the pelagic trawl were >35 mm DML and no animals >35 mm were caught in the IKMT.

Length-frequency distributions for *S. leucopsarus* and *T. crenularis* from both trawls (Figure 3) show that large lanternfishes are clearly undersampled by the IKMT. The modes composed of fishes >45 mm, which are prominent in pelagic trawl catches, are absent in IKMT catches.

Another notable example of differences between catches of large fish in these collections were captures of *Tactostoma macropus*. Few large individuals (>250 mm) have been collected in IKMT tows off Oregon. Three tows with the pelagic trawl at depths of 470-1,070 m in 1978, however, captured many large fish. Twenty-nine percent of the *T. macropus* caught in these pelagic trawl collections were >250 mm, compared with only 8.2% in 252 IKMT tows to 500 m depth or deeper during previous years.

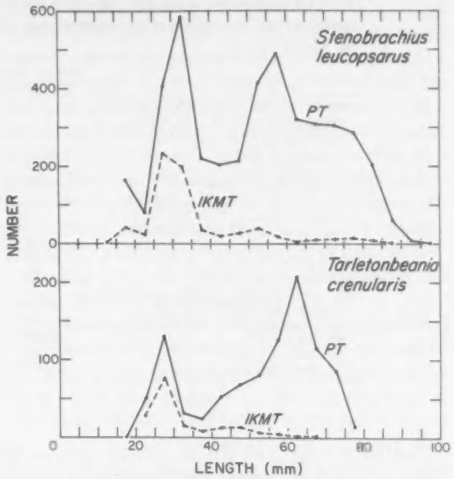

FIGURE 3.—Length-frequency distribution for *Stenobrachius leucopsarus* and *Tarletonbeania crenularis* in pelagic trawl and IKMT collections, July 1976, 0-500 m.

Effective Cross-Sectional Area of the Pelagic Trawl

The cross-sectional area of the pelagic trawl was indirectly estimated from the catches of four species of lanternfishes caught in both the pelagic trawl and IKMT on the three "paired" cruises (Table 1) to see how it compared with the divers' estimates of 50 m². The following equation was used:

$$A = \frac{C_1 V}{C_2 D}$$

where A = area in square meters,
C_1 = number of fish caught by pelagic trawl,
V = volume filtered by the IKMT, in cubic meters,
C_2 = number of fish caught by the IKMT,
D = distance trawled by the pelagic trawl in meters.

The volume of water filtered by the IKMT was calculated from a flowmeter mounted in the MPS and monitored aboard ship via electrical cable (see Pearcy et al. 1977). Distances trawled by the pelagic trawl were calculated from ship speed (based on Loran readings) and the duration of the tow. In each comparison, tows and nets selected fished similar depths at the same time of day. The mouth area estimated in this way varied from 19 to 3,161 m² with a median value between 48 and 62 m² (Table 3). The smallest area (19 m²), for *D. theta*, can be largely explained by the retention of small fish (10-15 mm) in the IKMT but not by the slightly larger mesh of the pelagic trawl. This is the only obvious example of differences in size-frequency distributions that can be explained by escapement of small fish. The large values of mouth area may result from different population densities of two species at the times of sampling during the 1977 cruises.

The present study indicates that large nets usually catch more individuals, and usually, but not always, more species and larger animals than small IKMT-type nets. Detailed quantitative comparisons are needed with nets of known cross-sectional areas, with similar mesh size, at the same depths and locations (Roper 1977). Large nets will never replace the smaller IKMT's and rectangular midwater trawls because of the specialized equipment needed to launch and re-

TABLE 3.—Estimates of the effective mouth size of the pelagic trawl (PT) based on estimated distance trawled (speed × time), the catches of four lanternfishes, and the catches of four lanternfishes and volumes for IKMT's on "paired" cruises.

Item	*Stenobrachius leucopsarus*	*Diaphus theta*	*Tarletonbeania crenularis*	*Protomyctophum thompsoni*
1975—1 PT, 5 IKMT, 340-350 m, day:				
Distance trawled by PT = 23,718 m				
Vol. filtered by IKMT = 435,210 m^3				
No. caught in PT	2,121	216	146	218
No. caught in IKMT	816	212	61	123
Effective mouth area, m^2	48	19	44	32
1976—8 PT, 11 IKMT, 0-350 m, day/night:				
Distance trawled by PT = 148,425 m				
Vol. filtered by IKMT = 1,525,860 m^3				
No. caught in PT	4,306	1,663	1,007	183
No. caught in IKMT	718	644	167	60
Effective mouth area, m^2	62	27	62	31
1977—2 PT, 3 IKMT, 290-325 m, day/night:				
Distance trawled by PT = 18,931 m				
Vol. filtered by IKMT = 630,385 m^3				
No. caught in PT	2,658	149	388	192
No. caught in IKMT	28	4	2	100
Effective mouth area, m^2	3,161	1,240	646	54

cover large nets from oceanographic vessels. We need to compare catches of different-sized trawls, however, in order to evaluate biases and to learn what portions of the plankton-micronekton-nekton spectrum are effectively sampled by different nets.

Acknowledgments

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PASSIVE BEHAVIOR BY THE SPOTTED DOLPHIN, *STENELLA ATTENUATA*, IN TUNA PURSE SEINE NETS

The purse seining method of catching yellowfin tuna, *Thunnus albacares*, in association with schools of dolphins in the eastern tropical Pacific has been described by Perrin (1969). The primary target species, in order of importance, are the spotted dolphin, *Stenella attenuata*, and the spinner dolphin, *S. longirostris*, with occasional net sets made on schools of the common dolphin, *Delphinus delphis*. Schools of these dolphins ranging in size from 50 to several thousand are herded with speedboats and encircled with a purse seine net that is from 900 to 1,400 m long and as much as 130 m deep. After the dolphins are encircled, the bottom of the net is pursed, entrapping the mammals and any tuna that are associated with the school. Presently, neither the mechanisms nor the function of the close association of the yellowfin tuna with these schools of dolphins in the eastern tropical Pacific are clearly understood.

Studies of the behavior of dolphins while captive in a purse seine net were pursued during the chartered cruise of the commercial seiner MV *Elizabeth C. J.*, in October 1976 (Norris et al.[1]). Prior to this cruise, however, beginning in 1973, an intensive effort was made to develop net modifications and fishing techniques that would decrease the incidental killing of the mammals. Much of this effort was based upon general, to date unpublished, observations of captured dolphins and tuna made by National Marine Fisheries Service (NMFS) observers and technologists. One of the behavioral patterns of the spotted dolphin first noted by NMFS divers in 1973 and then recognized for its contribution to incidental mortality in 1975 is termed here "passive" behavior.

In the fall of 1975, NMFS chartered the purse seiner MV *Bold Contender* to carry on fishing gear dynamics research aimed at reducing incidental dolphin mortality. Part of this research included the evaluation of the use of a two-man inflatable raft as a dolphin rescue platform during and after the release procedure known as the "backdown" (Perrin 1969; Coe and Sousa 1972). A face mask and snorkel were worn by the person in the rescue raft to enable him to: 1) signal when tuna were approaching the release area during backdown, 2) keep track of sharks, particularly the oceanic whitetip shark, *Carcharinus longimanus*, both inside and outside of the net, 3) locate and release any stray dolphins and, 4) observe the dynamics of the net modification being tested during the cruise. Notes on the behavior of the captured dolphins during backdown were recorded after each of the 25 net sets in which the rescue raft was used. The underwater passive behavior of spotted dolphins was first noted in the eighth net set of the cruise and in 14 subsequent sets.

The passive behavior manifests itself in possibly two forms during the backdown release procedure. The first, which has been described as "rafting" by Norris et al. (see footnote 1), consists of groups of 5-50 or more spotted dolphins hanging tail-down at or near the surface and showing no overt reactions to their surroundings. This type of passive behavior can be seen from the deck of the seiner and is generally displayed from the time the net is pursed through the backdown (about ½ h). There is a steady increase in the number of rafting animals until backdown begins and then an apparent sharp decrease as backdown proceeds. The decrease in rafting may be due to the crowding and confusion during that period. Rafting behavior simplifies the effective release of these animals by backdown, because the net is actually pulled out from under the "raft" of dolphins as it remains relatively stationary in the water. Observations during the *Elizabeth C. J.* cruise showed that in every school of captured spotted dolphins some portion exhibited this behavior.

Dolphins in the captured school that are not in rafts during backdown are either actively swimming, usually in the horizontal plane directly away from the advancing wall of the net, or display the second manifestation of passive behavior. Prior to backdown, rafting dolphins are occasionally observed to sink tail first to depths up to 5 m before they swim awkwardly back to the surface, breathe, and sink again. During backdown, however, there are occasionally relatively large numbers of animals that sink to lie on the webbing (Figure 1) and many more that show signs of the sinking behavior and drop out of the rafts.

During backdowns on the *Elizabeth C. J.* cruise, from 3 to an estimated 75 spotted dolphins and, in one set, 2 bottlenose dolphins, *Tursiops truncatus*, were observed lying on the webbing in the bottom of the backdown channel. These animals, which

[1]Norris, K. S., W. E. Stuntz, and W. Rogers. 1978. The behavior of porpoises and tuna in the eastern tropical Pacific yellowfin tuna fishery - preliminary studies. Available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va., as PB-283970, 86 p.

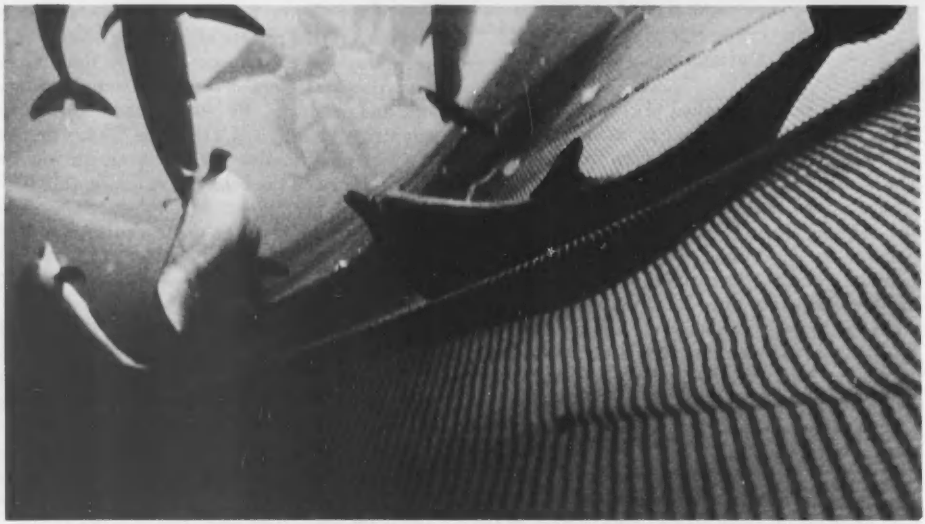

FIGURE 1.—Photograph taken during backdown of a tuna purse seiner showing three passive dolphins in the foreground. Note that the middle animal is resting on its dorsal fin. The four animals that are hanging flukes downward in the water are displaying the sinking behavior associated with rafting. (Photo courtesy of the Cooperative Dedicated Vessel Research Program, 1978.)

were making no apparent attempt to surface, were at depths that varied from 2 or 3 m to as much as 12 to 15 m. At first glance, the animals appeared to be struggling feebly, perhaps against the current being produced as the seine was pulled through the water during backdown. Their movements were weak and lacked the grace that long observation leads one to expect in dolphins. The majority of animals lying on the net in this manner were oriented with their heads toward the release area of the net (i.e., in the direction of the current), whereas the rafting and active animals were normally oriented away from the release area (i.e., heading into the current). After about 3-5 min, the passive dolphins began to rise singly or in two's and three's to breathe and were either backed out of the net or hand-released if the backdown procedure had already been terminated. No animals were seen returning to rest on the bottom of the net after surfacing.

Prior to promulgation and adoption of a federal regulation requiring use of a rescuer in a raft using a mask and snorkel, which resulted from the chartered cruise of the *Bold Contender*, this passive behavior probably was an important contributor to dolphin mortality in purse seines. When viewed from the deck of a speedboat tending the corkline in the dolphin-release area during backdown, these animals appeared to be dead if they were noticed at all, and as a result the release efforts were often prematurely terminated. Dolphins not released during the backdown have a high probability of being killed (Coe and DeBeer[2]).

The reasons for passive behavior in purse seine-caught spotted dolphins are not understood. The behavior has only rarely been observed in spinner dolphins in the tuna fishery. A similar behavior pattern has been described for two newly captured Hawaiian spinner dolphins during escape behavior experiments designed to delineate the dimensions of a dolphin release gate for possible use in purse seine nets (Perrin and Hunter 1972).

Animal trainers and biologists have noted what appears as similar behavior in individual captive dolphins of several species. Caldwell et al. (1966) reported prolonged inverted "resting or sleeping

[2]Coe, J. M., and J. DeBeer. 1977. Results of the 1976 twenty vessel test of two fine mesh systems to reduce incidental porpoise mortality in tuna purse seining. Unpubl. manuscr., 75 p. Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

on the bottom of the tank" by a juvenile male Boutu, *Inia geoffrensis*. The occurrence of this behavior in *I. geoffrensis* and that observed in a juvenile male Atlantic bottlenose dolphin was frequent and apparently spontaneous (Caldwell[3]). Pryor[4] and Norris et al. (footnote 1) have noted instances where the passive-type behavior was presumably induced in training situations where *Tursiops* spp. were being "worked hard." These animals would go to the bottom of the tank, emit a quantity of air and might remain at the bottom for several minutes. Norris et al. hypothesized that this behavior may be similar to the "dearoused state" described by Delius (1970) for terrestrial animals, the most widely known example of which is the feigning of death by the Virginia opposum, *Didelphis marsupialis*. The major criticism (Norris et al.) of the dearousal hypothesis in the present situation would seem to concern the evolutionary value of such a response to a pelagic air breathing animal that would tend to sink toward the bottom in very deep water. One argument (Norris et al.) is that the situation which elicits dearousal (purse seining) has been a factor for only about 15-20 yr, and it is therefore not necessary to hypothesize an adaptive value for the behavior. To accept this hypothesis it would have to be assumed that the capability for dearousal has evolved in response to other circumstances.

A second hypothesis to explain this behavior relates to the effects of chase and capture on the physiology of the dolphins. Possibly indicative is the awkwardness of the swimming movements displayed by the animals while "passive." Harthoorn (1973) described the effects of chase and capture on large African mammals. Long chases using motor-driven vehicles result in a typical condition termed "capture myopathy." Capture myopathy is very common in the animals captured for zoos and often causes a delayed mortality. Symptoms include stiffness and awkward movements. The method of capturing dolphin schools involves a chase by speedboats that lasts up to 1.5 h and averages between 20 and 30 min. A chase of that duration is capable of causing myopathies in large terrestrial mammals which can be detected by measuring changes in blood serum enzyme levels (Harthoorn). A recent paper by Colgrove (1978) documents a suspected case of myopathy in a dolphin, *Tursiops gilli* = *T. truncatus*. This case of myopathy appears to have been induced by the stress of transporting the animal. Investigation of blood chemistry of passive dolphins may allow determination of whether capture myopathy does occur as a result of chase and capture during the tuna seining operation.

[3]David K. Caldwell, Director, Biocommunication and Marine Mammal Research Facility, University of Florida, Route 1, Box 121, St. Augustine, FL 32084, pers. commun. October 1979.

[4]Karen Pryor, former head animal trainer, Sea Life Park, Hawaii; present address: 28 East 10th Street, New York, NY 10003, pers. commun. November 1976.

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EFFECTS OF LARGE PREDATORS ON THE FIELD CULTURE OF THE HARD CLAM, *MERCENARIA MERCENARIA*[1]

Individuals in the clam industry have used fences to keep the cownose ray, *Rhinoptera bonasus*, out of planted areas (Lewis[2]; Burton[3]). Tiller et al. (1952) indicated losses due to skates in planted holding areas and stated that "One man reported the loss of 600 bushels of small clams in two nights during 1948...." Merriner and Smith[4] stated that cownose ray predation is a serious problem on oyster and clam grounds in Chesapeake Bay. From these observations it is clear that such large predators could be a significant deterrent to the culture of clams from Delaware Bay southward along the Atlantic coast.

The present study continues a program designed to evaluate methods of protecting areas seeded with young *Mercenaria mercenaria*. The initial portion of the study outlined the interactive effects of pens, gravel, current baffles and crab traps on the first year's growth and survival (Kraeuter and Castagna 1977). The results of the second year study on the interactive effects of these manipulations are recorded below. The data indicate effectiveness of efforts to prevent predation on clams surviving the first year's plantings.

Methods

Details of the experimental design were presented in the previous paper (Kraeuter and Castagna 1977) and are briefly discussed below.

Four contiguous intertidal sites were marked by pushing stakes into the muddy substrate and two of the four sites were enclosed by 10 mm mesh plastic net 2.3 m high stretched around the 38 m circumference. The two remaining sites were left open (Figure 1). Crab traps were placed within one of the penned and one of the unpenned (no net) sites to assess the predatory effects of the blue crab, *Callinectes sapidus*. In addition, within each site, areas to be seeded were marked and designated to be treated with or without combinations of metal framed current baffles and crushed granite gravel. Current baffles 0.6 m high were constructed to decrease the scouring effects of currents. Since average tidal amplitudes are 1.2 m, the baffles did not prevent entrance of fish or crabs into the plots. Each baffle was about 1.5 m long and 12 baffles were set in an array forming four squares (Figure 1). Clam seed (about 2 mm) was planted in all sites at 3,000/m^2.

Clams were sampled in each site with a 7.4 cm diameter corer. A 0.6 m^2 grid was placed over each treatment and 10 random samples were removed in July 1977. This is a continuation of the previous year's sampling. For final sampling (October-November 1977), all sites were harvested using a suction sampler with an attached mesh bag. Four quadrats corresponding to the squares formed by placing current baffles in squares were sampled as discrete units (Figure 1). Where no baffles were utilized for the treatment, squares were marked by stakes and sampled as though the baffles had been present. All clams removed from the plots were brought to the laboratory, counted, and the percent commercial size (1 in (25.4 mm) thick New York legal limit) was determined. The data (counts) were transformed by $\log_{10}$ and compared by a factorial analysis of variance design (ANOVA).

Results and Discussion

Results from the first year sampling (through September 1976) indicated that baffles and gravel in combination were superior to any other treatment. Plots were sited in an area where predaceous echinoderms were not present, and although pens were not effective in preventing crab predation, no discernable damage could be attributed to other predators (Kraeuter and Castagna 1977).

The statistical summaries (Table 1) are a continuation of the table presented by Kraeuter and Castagna (1977), and, as in that paper, it is important to emphasize that the sampling results from one period to the next were not independent. The final data represent the cumulative effects of all environmental and biotic interactions on clams planted in fall 1975.

The July 1977 results mirrored those of earlier sampling periods (Kraeuter and Castagna 1977) with the exception that the pen × trap and pen × baffle × trap interactions were significant at the 0.05 level. This was due, in part, to the higher level of predation in the penned area without traps (18

[1]Contribution No. 924 from Virginia Institute of Marine Science.

[2]J. H. Lewis, seafood shipper and packer, Saxis, VA 23427, pers. commun. Nov. 1976.

[3]L. L. Burton, seafood shipper and packer, Burton's Seafood, Chincoteague, VA 23336, pers. commun. Sept. 1976.

[4]Merriner, J. V., and J. W. Smith. 1979. Gear feasibility study for the cownose ray, *Rhinoptera bonasus*. Va. Inst. Mar. Sci., Spec. Rep. Appl. Mar. Sci. Ocean Eng. 227, 27 p.

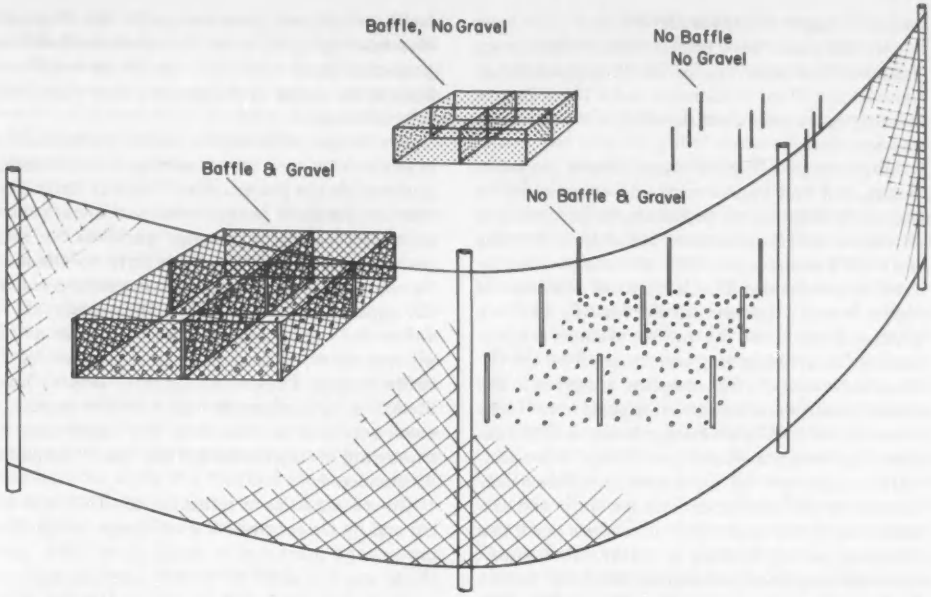

FIGURE 1.—Diagram of one site of the experimental design indicating the presence of each plot and the net for protection of juvenile *Mercenaria mercenaria*. Included in one site with a net would be a crab trap (not illustrated). The net was pushed into the substrate.

TABLE 1.—ANOVA table for survival of hard clam, *Mercenaria mercenaria*, juveniles with tests of pens, baffles, gravel, and traps and their interactions. Identical SS in the July data were caused by clams being absent in all sites with no baffle and no gravel.

	July 1977				October-November 1977			
Source of variation	df	SS	MS	*F*	df	SS	MS	*F*
Total	159	7.91			63	54.64		
Pens (P)	1	.02	0.02		1	4.31	4.31	114.31***
Baffles (B)	1	1.44	1.44	63.17***	1	32.17	32.17	853.37***
Gravel (G)	1	1.56	1.56	68.27***	1	10.21	10.21	270.89***
Traps (T)	1	.01	.01		1	.39	.39	10.43**
P × B	1	.05	.05		1	1.16	1.16	30.64***
P × G	1	.03	.03		1	2.76	2.76	73.30***
P × T	1	.09	.09	4.08*	1	.94	.94	24.90***
B × G	1	1.12	1.12	49.02***	1	.07	.07	
B × T	1	.00	.00		1	.01	.01	
G × T	1	.001	.001		1	.42	.42	11.12**
P × B × G	1	.08	.08		1	.04	.04	
P × B × T	1	.09	.09	4.05*	1	.001	.001	
P × G × T	1	.07	.07		1	.01	.01	
B × G × T	1	.004	.004		1	.17	.17	4.61*
P × B × G × T	1	.07	.07		1	.16	.16	4.20*
Residual	144	3.29	.02		48	1.81	0.04	

***$P<0.001$, **$P<0.01$, *$P<0.05$.

clams sampled vs. 31 clams sampled in penned areas with traps), and, in part, to predation at the no pen no trap site, 23 clams sampled vs. 15 clams at the no pen plus trap site. These data indicate that trapping is essential in penned areas, but that when pens are absent crab trapping is of no benefit.

Within 2 wk following the July sampling, inspection of the sites revealed that clams 1.5-4.0 cm high had been crushed. These shell fragments

were the result of large predators. The shells were clean and some were mixed within the surface layer on the bottom. In addition, the predators had created pits 50 cm in diameter and 6-10 cm deep in the aggregate and substrate which had been covering the clams.

To eliminate effects of losses due to predation during the first year's study and concentrate on the effects due to these predators, we have utilized the estimate of the mean number of clams from the July 1977 samples as 100% of those present for further predation. The estimated numbers of clams in each experimental plot for July 1977 are given in Table 2, and the number of clams remaining for the corresponding treatments from the October to November 1977 sampling are given in the same table. Several important aspects not evident from the ANOVA table are apparent. A combination of baffles, gravel, pens, and traps was essential for high survival. Pens were significant only because of the predation between July and October. The percentage survival between these two sampling periods seemed to indicate that gravel somehow negatively interacted with the baffles (compare percent survival B + G and B + NG, Table 2) when pens were absent. This was not the case, but resulted from heavy predation in the baffle + gravel sites with no pens. Since there were more clams in these areas in July, the percent survival was lower, but total survival was better than in the baffle + no gravel sites (Table 2). The higher survival in the baffled sites was due to the protection the baffles offered the clams when the predators entered the area. Almost all clams found in these areas were close to, or beneath, the cross rods supporting the bottom of the baffle. This same shadow effect was the cause of the nonsignificant baffle + gravel interaction in the October-November ANOVA table. If more clams had been present in the B + NG sites, the clams would have been in the center of the plot and thus vulnerable to predation.

The impact of predation to the mariculture of clams can be seen by comparing survival inside and outside the penned sites (Table 2). Estimated survival inside a penned area was always more than 76%, and the average survival for both penned sites was 94% from July to October-November. Average survival for the same period in the unpenned sites was 8.75%. The greatest survival in the unpenned areas was 65% but, as explained above, was due to protection provided by baffle frames. These data indicate that at least 85-90% of the observed losses in the unpenned sites were due to predation. The importance of these data is amplified when the size of the clams is considered.

The average size of clams in July 1977 was 3.2 cm and by October was 3.9 cm (hinge to lip). The percentage marketable clams (1 in (25.4 mm) thick) was the same for both the penned and unpenned sites (58.5 and 58.6%) in October. This indicates no size selection of clams, but that clams of all sizes were consumed. The loss of such large clams represents 2 yr of work and a product of market size.

Flounders, known to prey on young *Mercenaria mercenaria* and to selectively eat the neck of adult clams, have been eliminated as potential predators because they are not capable of crushing the shell of 3 cm high hard clams. Of the seven species of fish capable of forming pits and crushing the shell of 3 cm size hard clams (Table 3), only two are known to be common away from the inlets and near the planted areas (Richards and Castagna 1970; Musick 1972). These two species, *Dasyatis centroura* and *Rhinoptera bonasus*, are prime suspects for causing the destruction in our unprotected plots. The former cannot be eliminated be-

TABLE 2.—Total number of clams estimated from mean number per sample (July 1977), total counts (October-November 1977), and the percent mortality between the sampling dates. — = not calculated because of 0 estimate in July. P = pens, T = traps, G = gravel, B = baffle. The prefix N = absence; NP = no pen, etc.

Month or period	Item	B + G	NB + G	B + NG	NBNG
July 1977	P + T	6,670	230	230	0
	P + NT	4,140	0	0	0
	NP + T	2,760	460	230	0
	NPNT	4,830	230	230	0
Oct.-Nov. 1977	P + T	6,723	174	352	2
	P + NT	3,228	23	126	2
	NP + T	257	17	75	2
	NPNT	248	13	148	5
% survival	P + T	101	76	153	—
July to Oct.-Nov.	P + NT	78	—	—	—
	NP + T	9	4	33	—
	NPNT	5	6	65	—

TABLE 3.—Potential fish predators on 3 cm hard clams in Virginia. Information from Richards and Castagna (1970) and Musick (1972).

Scientific name	Common name
Dasyatis americana	Southern stingray
D. centroura	Roughtail stingray
D. sayi	Bluntnose stingray
Myliobatis freminvillei	Bullnose ray
Aetobatus narinari	Spotted eagle ray
Rhinoptera bonasus	Cownose ray
Pogonias cromis	Black drum

cause of its large size and overall abundance within the area and the latter because of its schooling behavior. Schools of *R. bonasus* often destroy large areas of eelgrass and other habitats in search of clams, their primary food (Orth 1975, 1977). Burton (footnote 3) used hog wire fencing to keep schools of cownose rays from his beds of inventoried and replanted market size *Mercenaria*. Because of the suddenness of the disappearance (<2 wk) and the presence of crushed clam shell in this and other plantings, we believe the most likely predator was a school of *R. bonasus*.

Our data indicate that losses, due to such predation, would be unpredictable, but it would be financially devastating to the clam grower. The use of a fence or some other device to protect the clams is essential for successful field culture in areas where large predators occur. These fences can be removed during the winter to prevent ice damage, but along the Virginia coast they should be kept in place and maintained at all times from late March to early November.

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A DIRECT METHOD FOR ESTIMATING NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, SPAWNING BIOMASS

Two methods exist for estimating spawning biomass, the total weight of mature fish, from abundance of spawning products. The first, or direct, method (Saville 1963) consists of dividing an estimate of egg production by the product of batch fecundity and the proportion of females in the mature stock. Saville safely assumed spawning frequency to be unity. The second method is indirect (Murphy 1966; Smith 1972) and utilizes information from two different species. Smith illustrated the second method, using information on the Pacific sardine, *Sardinops caerulea*, and northern anchovy, *Engraulis mordax*. Sardine spawner biomass is estimated from landings data and cohort analysis; anchovy spawner biomass is estimated by multiplying the estimated sardine spawner biomass by the product of the anchovy-to-sardine ratio of larval abundance and the sardine-to-anchovy ratios of fecundity, and spawning frequency. Computation was facilitated by assuming the unknown spawning frequencies to be equal, making the ratio of spawning frequencies unity. Up to the present only the second method has been used for the northern anchovy. This paper presents estimates derived from the first.

Computation of spawning biomass is simplified for the direct method when spawning occurs but once and for the indirect method when both species spawn with equal frequency. Difficulties arise when spawning is continuous and when it cannot be safely assumed that all mature fish spawn with the same frequency. This is the case with the northern anchovy. Spawning products are present all year, with a maximum abundance occurring in the late winter and early spring and a minimum during late summer and early fall. Abundance of and seasonal pattern of spawning products give no clue as to the number of spawnings by size and age, or even to the average number of spawnings.

Under the following conditions spawning frequency can be estimated from examining the spawning condition of females: 1) females can be examined for a characteristic that indicates when spawning takes place; 2) the length of time such a characteristic remains detectable can be estimated; 3) the spawning rate remains relatively constant over the sampling interval.

The spawning fraction, or frequency, is the

fraction of females displaying the characteristic divided by the length of the time interval the characteristic remains detectable. Say, from a sample of 10 females, 2 display a characteristic which lasts for 1 day and which indicates that spawning will take place in approximately 1 wk. The daily spawning fraction 1 wk hence will be 1/5.

Given this method for estimating spawning fraction the following relationship holds:

$$P = S(abc) \tag{1}$$

where P = production in eggs,
a = batch fecundity in (eggs)/(unit weight),
b = fraction spawning (weight of spawning females)/(weight of all mature females),
c = (weight of females)/(weight of spawning stock),
S = spawning biomass.

Spawning biomass can be estimated directly:

$$S = P(abc)^{-1}. \tag{2}$$

Hunter and Goldberg (1979) examined female northern anchovies for characteristics that would indicate a recent spawning. They found that following spawning follicles of the northern anchovy go through a sequence of identifiable degenerative stages. The first two stages, which Hunter and Goldberg referred to as day 0 and day 1, have durations of 1 day. Stage identification is subject to error. Day-0 follicles can be misidentified as day 1; day-1 follicles can be misidentified as day 2 and beyond. The most easily identified stage is day 1. If the spawning fraction, b, is based on day-1 follicles an adjustment factor, say d, is required in Equation (2):

$$S = P(ab'c)^{-1}d \tag{3}$$

where b', replacing b, is the observed fraction.

The adjustment factor is computed by using information on the fraction of day-0 follicles misclassified as day 1, say d_0, and the fraction of day-1 follicles correctly classified, say d_1.

$$d = (d_0 + d_1)$$
$$\mathrm{Var}(d) = \mathrm{Var}(d_0) + \mathrm{Var}(d_1).$$

Estimates based on Hunter and Goldberg's (1979, table 1) blind classification study for d_0 and d_1 are 5/21 and 16/19 respectively; hence

$$d = 1.080$$
$$\mathrm{Var}(d) = 0.016.$$

From examination of 195 females taken by midwater trawl during the time interval 15-27 February 1978, Hunter and Goldberg estimated the observed daily spawning fraction and its variance:

$$b' = 0.159$$
$$\mathrm{Var}(b') = 4.561 \times 10^{-4}.$$

Based on the total female weight of nonspawners the estimated batch fecundity and variance are from Hunter and Goldberg (1979, table 6)

$$a = 396 \text{ eggs/g (or } 3.96 \times 10^{8} \text{ eggs/t)}$$
$$\mathrm{Var}(a) = 886.$$

For the time period 18 February-17 March 1978, Zweifel[1] estimated daily egg production. From 177 plankton samples, northern anchovy eggs and larvae were staged from time of spawning. Estimated total numbers at stage were regressed on time. The ordinate intercept, number at time zero, is the estimated egg production:

$$P = 2.321 \times 10^{13} \text{ eggs/d}$$
$$\mathrm{Var}(P) = 1.825 \times 10^{26}.$$

If the female to male sex ratio in numbers were 1:1 and if the two sexes had equal growth rates in terms of weight then c could be assumed to be 0.5. However, because of conflicting and insufficient evidence neither of these two hypotheses can be supported. Klingbeil (1978) demonstrated that the distribution of northern anchovy sexes is heterogeneous over space and time and that estimates of sex ratio are dependent on the sampling gear. From the purse seine fishery Klingbeil estimated that the ratio of numbers of females to males varies between 1.14:1 and 2.02:1 for 1969-76. From 9 yr of midwater trawl data Klingbeil estimated that the sex ratio is 1.03:1. Since midwater trawl surveys cover a wider geographic area and size range of anchovies, they probably provide an estimate closer to that of the true population sex ratio. However, since neither midwater trawl surveys

[1]James Zweifel, Southwest Fisheries Center La Jolla Laboratory, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun.

nor purse seines are designed to estimate sex ratio it can only be stated that the anchovy sex ratio has not been adequately estimated.

Collins (1969) showed that females are greater in length and weight at age than males. However, since Collins' estimates are based on combined data from three fishing seasons and, since female weights are known to fluctuate within season due to spawning activity, the precision with which the data can be used for estimation purposes is open to speculation.

For the present purpose of estimating c the sex ratio of the number of females to males plus females as estimated from the February 1978 midwater trawl survey (Hunter and Goldberg 1979) will be used. Reexamining original data used by Hunter and Goldberg (1979, table 5) the ratio estimate is

$$\begin{aligned} c &= 0.550 \\ \mathrm{Var}(c) &= 0.001. \end{aligned}$$

This assumes, of course, an equal weight at age.

In the future, the best estimate of c is likely to be the ratio of the actual sampled weights of males and females; these were not available for the February 1978 survey. This would, of course, require the assumption that the sex ratio can differ from 1:1, that the weight distribution of the two sexes can change with time, and that a sample estimate is a better estimate than any hypothesized or long-term average value.

Using the following estimates

$$\begin{aligned} P &= 2.321 \times 10^{13} \text{ eggs/d} & c &= 0.550 \\ a &= 3.96 \times 10^{8} \text{ eggs/t} & d &= 1.080 \\ b' &= 0.159 \end{aligned}$$

the estimated S is approximately 0.72 million t. This is reasonably close to the estimate by the Smith procedure (Stauffer and Parker[2]) of 1.17 t.

At this time caution should be exercised in interpreting the general range described by these two estimates. The parameters of Smith's procedure have not been formally estimated. The parameter estimates of this new method are only first approximations. P may not be constant for as long a time interval as assumed here. Observed b' was found to be consistent for time of day, weight of fish, and geographic location. This may not prove to be the case under more intensive sampling. Another problem in estimating the spawning fraction is in determining female sexual maturity. This problem may be particularly acute for recently spawned young females where microscopic analysis is necessary to separate the recently spawned from the sexually immature. Misclassifying recently spawned as immature would tend to inflate the estimated b.

By the delta method (Seber 1973), the variance of S is

$$\mathrm{Var}(S) = (ab'c)^{-2}\left[d^2\mathrm{Var}(P) + P^2\mathrm{Var}(d) + (Pd)^2\left[\frac{\mathrm{Var}(a)}{a^2} + \frac{\mathrm{Var}(b')}{b'^2} + \frac{\mathrm{Var}(c)}{C^2}\right]\right]. \quad (4)$$

Dividing Equation (4) by the square of Equation (3) and then taking the square root we have the coefficient of variation (CV) of spawning biomass

$$\mathrm{CV}(S) = \sqrt{[\mathrm{CV}(P)]^2 + [\mathrm{CV}(a)]^2 + [\mathrm{CV}(b)]^2 + [\mathrm{CV}(c)]^2 + [\mathrm{CV}(d)]^2}, \quad (5)$$

which is the component vector of the coefficients of variation of the estimated parameters, right side of Equation (3). Since possible covariance terms are neglected, Equation (5) may be somewhat oversimplified. However, Equation (5) allows a first approximation to delegating the relative impact of the precision of the individual parameter estimates. The squared coefficients of variation are as follows:

$$\begin{aligned} [\mathrm{CV}(P)]^2 &= 0.339 & [\mathrm{CV}(c)]^2 &= 0.003 \\ [\mathrm{CV}(a)]^2 &= 0.005 & [\mathrm{CV}(d)]^2 &= 0.013. \\ [\mathrm{CV}(b)]^2 &= 0.018 \end{aligned}$$

Thus $\mathrm{CV}(S) = 0.614$. P contributes approximately 8 times more to the coefficient of variation of the spawner biomass estimate than all other parameters combined. In the future, additional effort will be allocated to estimating production.

The utility of the direct method, Equation (2), lies in the fact that all the parameters can be estimated. The same samples used for estimating b' can be used to estimate a and c. This can be done with 2 wk of midwater trawling. It is hoped

[2]Stauffer, G. S., and K. R. Parker. 1978. Estimate of the spawning biomass of the northern anchovy central subpopulation for the 1978-79 fishing season. U.S. Dep. Commer., NOAA, NMFS/SWFC Adm. Rep. LJ-78-9, 10 p.

that precise estimation of production can be done within 30 d by sampling for eggs; this goal seems attainable for the northern anchovy. Utilization of the method for other species seems feasible.

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FOOD OF THE HARBOR SEAL, *PHOCA VITULINA RICHARDSI*, IN THE GULF OF ALASKA

The harbor seal, *Phoca vitulina richardsi* (Shaughnessy and Fay 1977), is the most abundant and widespread coastal pinniped in the Gulf of Alaska. Harbor seals occupy virtually all nearshore habitats, and individuals occasionally occur as far as 100 km offshore (Spalding 1964; Wahl 1977; Fiscus et al.[1]). Despite their abundance and ecological importance, little information is available on their diet in Alaskan waters. In the most extensive food study published to date, Imler and Sarber (1947) examined stomachs of 99 seals from southeastern Alaska and 67 from the Copper River Delta. Wilke (1957) presented information on the food of seven harbor seals collected from Amchitka Island in the western Aleutian Islands. Kenyon (1965) reported on the stomach contents of 11 harbor seals taken in the same location. Bishop (1967) commented on stomach contents of two seals from Aialik Bay and two from Tugidak Island. Virtually no information has been available on the food of harbor seals from the Gulf of Alaska.

The study area (Figure 1) included coastal Gulf of Alaska from Yakutat Bay to Sanak Island. The portion of Cook Inlet north of Kachemak and Kamishak Bays was not included. The study area was divided into seven subareas for data analysis: northeastern Gulf of Alaska, Copper River Delta, Prince William Sound, Kenai coast, Lower Cook Inlet, Kodiak, and Alaska Peninsula.

Selection of Valdez as terminus of the trans-Alaskan oil pipeline and planned outer continental shelf oil and gas lease sales were the principal motivating factors for conducting this research. Production and transport of crude oil appeared to have the potential for significant alteration of the marine biota (Evans and Rice 1974) thus influencing the abundance and composition of harbor seal prey species. Established commercial fisheries for salmon, *Oncorhynchus* spp.; Pacific herring, *Clupea h. harengus*; halibut, *Hippoglossus stenolepis*; king crab, *Paralithodes camtschatica*; snow crab, *Chionoecetes bairdi*; Dungeness crab, *Cancer magister*; and shrimp, *Pandalus* spp., occur over the area, and pinnipeds are sometimes considered to be significant competitors with these fisheries. Data are needed to establish the possible impact of harbor seals on these commercially exploited species. Plans for developing fisheries are required by Federal laws (Public Law 94-265, Fishery Conservation and Management Act of 1976, and Public Law 92-522, Marine Mammal Protection Act of 1972) to utilize an integrated ecosystem approach to management

[1]Fiscus, C. H., H. W. Braham, R. W. Mercer, R. D. Everitt, B. D. Krogman, P. D. McGuire, C. E. Peterson, R. M. Sonntag, and D. E. Withrow. 1976. Seasonal distribution and relative abundance of marine mammals in the Gulf of Alaska. *In* Environmental assessment of the Alaskan Continental Shelf. Vol. 1. Principal investigators reports for October-December 1976, p. 19-264. Environmental Research Laboratories, NOAA, Boulder, Colo.

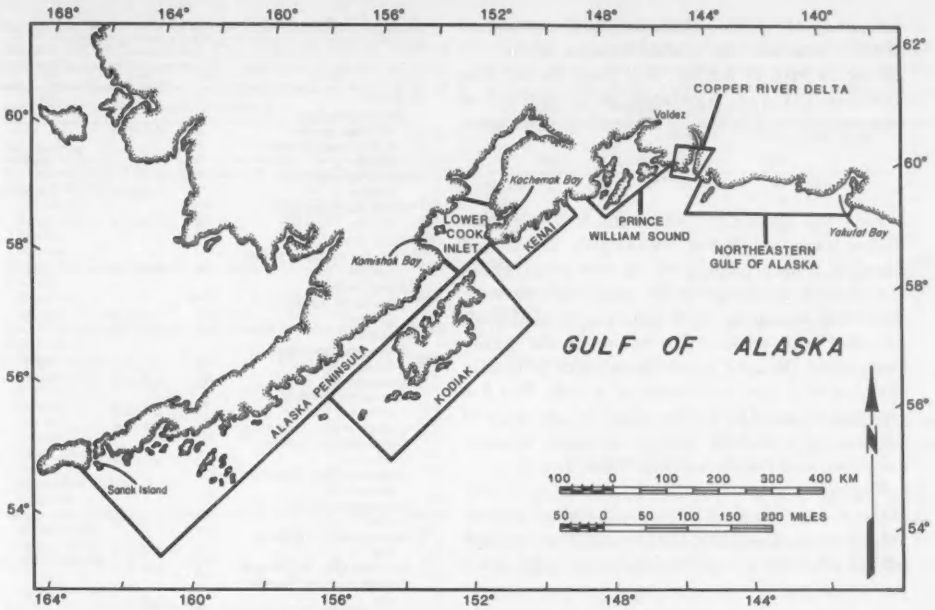

FIGURE 1.—Geographic subdivisions of Gulf of Alaska study area.

considering marine mammal populations as well as fishery resources.

Methods

A total of 548 harbor seals were collected by rifle throughout the Gulf of Alaska from 1973 through 1978 (Table 1). Reasonably complete seasonal coverage was obtained for Prince William Sound and the Kodiak area. Stomach contents were removed in the field, wrapped in muslin, and preserved in 10% Formalin.[2] In the laboratory the volumes and number of occurrences (number of stomachs in which a prey species was found) were determined for prey species. Because digestion was often advanced, skeletal materials, particularly fish otoliths and cephalopod mandibles (beaks), were the primary criteria for identification (Fitch and Brownell 1968; Pinkas et al. 1971).

Otoliths and other skeletal components from fish were tentatively identified to the lowest taxonomic level possible by comparison with reference materials. Otolith identifications were verified by John E. Fitch, California Department of Fish and Game, Long Beach. Cephalopod beaks were classified as either squid or octopus with the aid of Pinkas et al. (1971), and squid beaks were identified to family by Clifford H. Fiscus, National Marine Fisheries Service, NOAA, Seattle, Wash. Decapod crustaceans were identified by Kathryn J. Frost and Lloyd F. Lowry, Alaska Department of Fish and Game, Fairbanks.

In order to integrate data on both frequency of occurrence and prey volumes into a single ranking of prey utilization I used a modified form of the Index of Relative Importance (IRI)[3] devised by

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Geographic and seasonal distribution of harbor seals collected in the Gulf of Alaska.

Area	Number of seals			
	Jan.-Mar.	Apr.-June	July-Sept.	Oct.-Dec.
Northeastern Gulf of Alaska	—	22	—	9
Copper River Delta	—	18	27	—
Prince William Sound	62	24	26	39
Kenai coast	43	14	—	3
Lower Cook Inlet	—	37	—	—
Kodiak	4	106	38	53
Alaska Peninsula	—	20	3	—

[3]Original Index of Relative Importance as derived by Pinkas et al. (1971) was calculated by summing the numerical and volumetric percentage values and multiplying by the frequency of occurrence percentage value.

Pinkas et al. (1971). The numerical component of their formula was deleted because of the disparity in size of harbor seal prey items. The modified IRI was calculated as percentage of occurrences multiplied by percentage of volume.

Results

Food was present in 269 of the 548 stomachs. Fishes composed 74.5%, cephalopods 21.5%, and decapod crustaceans 4.0% of the occurrences (Table 2). A minimum of 27 species of fish were identified belonging to 13 families. Cephalopods included both octopus and squids of the family Gonatidae. Decapod crustaceans were primarily shrimps with one occurrence of a crab. The five top-ranked prey of harbor seals in the Gulf of Alaska were walleye pollock, octopus, capelin, eulachon, and Pacific herring (Table 3).

Regarding prey utilization by area of collection (Table 4), sample sizes were small and collections did not span all seasons (Table 1). Either walleye pollock or octopus was the top-ranked food in all marine areas and eulachon was dominant in the estuarian and freshwater habitats of the Copper River Delta. Walleye pollock was the top-ranked item in the eastern areas: northeastern Gulf of Alaska, Prince William Sound, and the Kenai coast. In the western areas: Lower Cook Inlet, Kodiak, and the Alaska Peninsula, octopus had the highest ranking. In Lower Cook Inlet, octopus and shrimps made up over 60% of both total

TABLE 2.—Stomach contents of 269 harbor seals collected in the Gulf of Alaska, all areas and seasons combined. [% under Occurrences = Percentage of occurrences and 95% confidence limits.]

Prey	Occurrences No.	Occurrences %	Volume ml	Volume %
Cephalopoda:	97	21.5±3.9	20,433	20.0
Octopus sp., octopus	77	17.1±3.5	18,753	18.3
Gonatidae, squids	20	4.4±2.0	1,680	1.6
Decapoda:	18	4.0±1.9	3,800	3.7
Shrimps	17	3.8±1.9	3,400	3.3
Crabs	1	0.2±0.5	400	0.4
Rajidae:				
Raja spp., skates	3	0.7±0.9	2,780	2.7
Clupeidae:				
Clupea h. harengus, Pacific herring	29	6.4±2.4	6,560	6.4
Salmonidae:				
Oncorhynchus spp., salmon	9	2.0±1.4	4,477	4.4
Osmeridae:	67	14.9±3.4	23,034	22.5
Mallotus villosus, capelin	40	8.8±2.7	10,687	10.4
Thaleichthys pacificus, eulachon	22	4.9±2.1	11,837	11.6
Hypomesus pretiosus, surf smelt	4	0.9±1.0	460	0.4
Unidentified Osmeridae, smelts	1	0.2±0.5	50	<0.1
Gadidae:	134	29.7±4.3	26,603	26.0
Eleginus gracilis, saffron cod	5	1.1±1.1	395	0.4
Gadus macrocephalus, Pacific cod	28	6.2±2.3	3,240	3.2
Microgradus proximus, Pacific tomcod	7	1.6±0.7	1,030	1.0
Theragra chalcogramma, walleye pollock	94	20.8±3.9	21,938	21.4
Zoarcidae:				
Lycodes spp., eelpouts	6	1.3±1.2	60	0.1
Scorpaenidae:				
Sebastes spp., rockfishes	4	0.9±1.0	810	0.8
Hexagrammidae:				
Hexagrammos spp., greenlings	2	0.4±0.7	400	0.4
Cottidae:	10	2.2±1.5	1,912	1.9
Dasycottus setiger, spinyhead sculpin	2	0.4±0.7	—	—
Enophrys bison, buffalo sculpin	1	0.2±0.5	240	0.2
Myoxocephalus spp., sculpins	2	0.4±0.7	1,430	1.4
Unidentified Cottidae, sculpins	5	1.1±1.1	242	0.2
Trichodontidae:				
Trichodon trichodon, Pacific sandfish	10	2.2±1.5	3,025	3.0
Bathymasteridae:				
Bathymaster signatus, searcher	3	0.7±0.9	40	<0.1
Ammodytidae:				
Ammodytes hexapterus, Pacific sand lance	19	4.2±2.0	463	0.5
Pleuronectidae:	23	5.3±2.2	2,615	2.6
Atheresthes stomias, arrowtooth flounder	3	0.7±0.9	—	—
Eopsetta jordani, petrale sole	1	0.2±0.5	—	—
Glyptocephalus zachirus, Rex sole	1	0.2±0.5	150	0.1
Hippoglossoides elassodon, flathead sole	5	1.1±1.1	130	0.1
Lepidopsetta bilineata, rock sole	1	0.2±0.5	—	—
Limanda aspera, yellowfin sole	6	1.3±1.2	1,650	1.6
Lyopsetta exilis, slender sole	2	0.4±0.7	—	—
Parophrys vetulus, English sole	2	0.4±0.7	65	<0.1
Unidentified Pleuronectidae	2	0.4±0.7	620	0.6
Unidentified fish remains	17	3.8±1.9	5,320	5.2
Totals	451	100.0	102,332	100.1

TABLE 3.—Rankings by modified Index of Relative Importance (IRI, see text footnote 3) of major prey of harbor seals collected in the Gulf of Alaska. Only those prey with IRI ≥2 are included.

Rank	Prey	Modified IRI	Occurrences (%)	Volume (%)
1	Walleye pollock	445	20.8	21.4
2	Octopus	313	17.1	18.3
3	Capelin	92	8.8	10.4
4	Eulachon	57	4.9	11.6
5	Pacific herring	41	6.4	6.4
6	Pacific cod	20	6.2	3.2
7.5	Flatfishes	13	5.1	2.6
7.5	Shrimps	13	3.8	3.3
9	Salmon	9	2.0	4.4
10	Squids	7	4.4	1.6
11	Pacific sandfish	7	2.2	3.0
12	Sculpins	4	2.2	1.9
14	Skates	2	0.7	2.7
14	Pacific sand lance	2	4.2	0.5
14	Pacific tomcod	2	1.6	1.0

TABLE 4.—Major prey of harbor seals from seven geographic areas in the Gulf of Alaska. Prey ranked in order of modified Index of Relative Importance (IRI, see text footnote 3). Only prey with IRI ≥2 are included. [Occurrences = Percentage of occurrences ± 95% confidence limits.]

Area and prey	IRI	Occurrences	Volume (%)
Northeastern Gulf of Alaska (stomachs with contents 17; occurrences 39; volume 2,420 ml)			
Walleye pollock	640	28.2±15.4	22.7
Surf smelt	196	10.3±10.8	19.0
Capelin	143	23.1±14.5	6.2
Shrimps	131	2.6± 6.3	50.4
Copper River Delta (stomachs with contents 14; occurrences 15; volume 8,115 ml)			
Eulachon	8,826	93.3±17.4	94.6
Salmon	36	6.7±17.4	5.4
Prince William Sound (stomachs with contents 83; occurrences 122; volume 28,290 ml)			
Walleye pollock	1,375	29.5± 8.5	46.8
Pacific herring	166	14.8± 6.7	11.2
Squids	77	13.1± 6.4	5.9
Octopus	75	13.9± 6.6	5.4
Salmon	33	3.3± 3.6	10.0
Capelin	16	4.1± 3.9	3.8
Pacific tomcod	5	1.6± 2.7	3.3
Pacific cod	4	4.9± 4.2	0.9
Saffron cod	3	2.5± 3.2	1.3
Eulachon	3	1.6± 2.7	1.9
Kenai coast (stomachs with contents 30; occurrences 52; volume 7,225 ml)			
Walleye pollock	1,503	40.4±14.3	37.2
Pacific herring	247	11.5± 9.6	21.5
Pacific sandfish	44	7.7± 8.2	5.7
Capelin	19	5.8± 7.3	3.3
Pacific tomcod	4	3.8± 6.2	1.0
Lower Cook Inlet (stomachs with contents 17; occurrences 23; volume 5,412 ml)			
Octopus	1,697	39.1±23.4	43.4
Eulachon	532	17.4±18.6	30.6
Shrimps	501	21.7±20.0	23.1
Capelin	17	8.7±14.4	1.9
Kodiak Island (stomachs with contents 102; occurrences 192; volume 42,685 ml)			
Octopus	631	21.4± 6.1	29.5
Capelin	323	10.9± 4.7	21.3
Walleye pollock	70	12.0± 4.9	5.8
Flatfishes	63	10.9± 4.7	5.8
Pacific cod	55	8.3± 4.2	6.6
Pacific sand lance	9	8.3± 4.2	1.1
Pacific herring	9	2.1± 2.3	4.2
Shrimps	8	3.6± 2.9	2.2
Salmon	6	2.1± 2.3	2.9
Sculpins	3	4.2± 3.1	0.7
Eulachon	2	0.5± 1.3	4.6
Alaska Peninsula (stomachs with contents 6; occurrences 9; volumes 8,185 ml)			
Octopus	929	33.3±41.8	27.9
Walleye pollock	824	22.2±37.5	37.1
Pacific sandfish	342	11.1±29.7	30.8
Pacific cod	40	22.2±37.5	1.8
Sculpins	26	11.1±29.7	2.3

occurrences and volumes which was nearly twice the percentages in other areas.

Chi-square analyses of prey occurrences for Kodiak Island and Prince William Sound indicated that in Prince William Sound more walleye pollock ($P<0.01$) were eaten than in Kodiak (Table 5). In Kodiak there was higher utilization ($P<0.05$) of capelin than in Prince William Sound. Octopus and Pacific cod were not utilized at significantly different rates ($P>0.05$). While samples were inadequate for statistical testing, it appeared that more squids and Pacific herring and

TABLE 5.—Comparison of occurrences of principal prey ($N\geq4$) of harbor seals collected in Prince William Sound and the Kodiak Island area. Statistical comparisons were made by chi-square analysis. [% = Percentage ± 95% confidence limits; — = Inadequate sample for statistical testing.]

Prey	Kodiak		Prince William Sound		
	No.	%	No.	%	P
Octopus	41	21.4±6.1	17	13.9±6.5	>0.05
Squids	2	1.0±1.7	16	13.1±6.4	—
Shrimps	7	3.6±2.9	1	0.8±2.0	—
Pacific herring	4	2.1±2.3	18	14.8±6.7	—
Salmon	4	2.1±2.3	4	3.3±3.6	—
Capelin	21	10.9±4.7	5	4.1±3.9	<0.05
Pacific cod	16	8.3±4.2	6	4.9±4.2	>0.10
Walleye pollock	23	12.0±4.9	36	29.5±8.5	<0.01
Sculpins	8	4.2±3.1	0	0.0	—
Pacific sand lance	16	8.3±4.2	0	0.0	—
Flatfishes	21	10.9±4.7	1	0.8±2.0	—
Total occurrences	192		122		

fewer Pacific sand lances, flatfishes, and sculpins were eaten in Prince William Sound than in Kodiak.

Salmon were found in the diet of harbor seals from both Prince William Sound and the Kodiak Island area only during the summer (Table 6). In the Kodiak area, feeding on Pacific sand lance appeared to be greatest in the fall while use of capelin seemed to peak in the spring. Use of Pacific herring by harbor seals appeared greatest in the spring in Prince William Sound.

Prey items were found in the stomachs of 13 harbor seal pups 2.5-11 mo of age and included shrimps, capelin, Pacific tomcod, walleye pollock, and Pacific sand lance. All items were <15 cm total length.

Discussion

The high ranking of walleye pollock in the harbor seal diet may have been a direct function of its abundance. Pereyra and Ronholt[4] found that walleye pollock was the dominant fish species in the Gulf of Alaska, composing 45% by weight of total fish stocks. Octopus, the second-ranked prey, appears to be an important food of harbor seals throughout the eastern North Pacific as nearly all food studies have found them to be a major component of the diet (Scheffer and Sperry 1931; Imler and Sarber 1947; Fisher 1952; Wilke 1957; Spalding 1964; Kenyon 1965; Bishop 1967). Five of the six, top-ranked prey were off-bottom, schooling fishes. Use of this type of prey may minimize

[4]Pereyra, W. T., and L. L. Ronholt. 1976. Baseline studies of demersal resources of the northern Gulf of Alaska shelf and slope. U.S. Dep. Commer., NOAA Processed Rep. NMFS NWFC, 281 p.

TABLE 6.—Seasonal occurrences of principal prey ($N \geq 4$) of harbor seals from the Kodiak Island area and Prince William Sound. [No. = Occurrences of prey; % = Percentage and 95% confidence limits.]

	Jan.-Mar.		Apr.-June		July-Sept.		Oct.-Dec.	
Area and prey	No.	%	No.	%	No.	%	No.	%
Kodiak Island area:								
Octopus	0	0.0	24	25.8± 9.4	6	15.0±12.3	9	15.8±10.3
Salmon	0	0.0	0	0.0	4	10.0±10.5	0	0.0
Capelin	0	0.0	14	15.1± 7.8	3	7.5± 9.4	3	5.3± 6.7
Pacific cod	0	0.0	8	8.6± 6.2	3	7.5± 9.4	4	7.0± 7.5
Walleye pollock	0	0.0	15	16.1± 8.0	3	7.5± 9.4	6	10.5± 8.8
Pacific sand lance	0	0.0	0	0.0	3	7.5± 9.4	12	21.1±11.5
Total occurrences	2		93		40		57	
Prince William Sound:								
Octopus	9	15.8±10.3	2	15.4±21.6	2	14.3±20.1	5	13.2±12.1
Squids	8	14.0± 9.9	0	0.0	3	21.4±23.5	5	13.2±12.1
Herring	8	14.0± 9.9	5	38.5±29.2	2	14.3±20.1	2	5.3± 8.4
Salmon	0	0.0	0	0.0	4	28.6±25.9	0	0.0
Capelin	4	7.0± 7.5	0	0.0	1	7.1±14.7	0	0.0
Walleye pollock	15	26.3±12.3	4	30.8±27.7	1	7.1±14.7	15	39.5±16.9
Total occurrences	57		13		14		38	

foraging effort and conserve energy compared with selection of more solitary species (Smith and Gaskin 1974).

The major differences in prey utilization between Prince William Sound and Kodiak are not readily explainable. However, water depths and topography for the two areas are considerably different (U.S. Department of Commerce[5]). Kodiak waters have considerable shallow shelf area, particularly east and south of the Island, and Prince William Sound generally has a rocky, precipitous coast and deep waters reaching 740 m. These features may influence prey composition, abundance, and availability to harbor seals.

Differential utilization of certain prey by season appeared to be explained by availability in most instances. Salmon occurred in stomachs of seals from both Kodiak and Prince William Sound only during the summer. In both areas salmon are only available in quantity in nearshore waters during this period. The apparent increases during spring in utilization of herring in Prince William Sound and capelin in the Kodiak area probably reflected nearshore distribution associated with spawning in these species (Hart 1973; Jangaard 1974). In the Kodiak area, Pacific sand lance were utilized to a greater extent during fall. No reason is known for this.

Six of the 10, top-ranked prey; walleye pollock, Pacific herring, Pacific cod, flatfishes, shrimps, and salmon are either currently harvested commercially or may be harvested in the near future (North Pacific Fishery Management Council[6]). Of particular interest is the possibility of increased harvests of walleye pollock which was the top-ranked prey of harbor seals accounting for about 21% of both total occurrences and volumes of food items. Sergeant (1976) believed that fisheries could compete with natural predators and cause their populations to stabilize at levels well below those existing prior to the fishery.

Harbor seals are present on the Copper River Delta from May through September. The results of this study and those of Imler and Sarber (1947) indicated that eulachon was the dominant prey from late May to mid-July. Nothing is known about feeding during late summer and fall when eulachon are not present.

Although specialized feeding on shrimps by newly weaned harbor seal pups was reported by Havinga (1933), Fisher (1952), and Bigg (1973), small fishes were the primary food of young seals <1 yr old collected during this study.

During this study several sampling problems and prey identification biases became apparent. Distinct geographic and seasonal variations in prey utilization were found to occur and because of this it was difficult to determine if a completely representative sample was obtained. Also, our sampling was restricted to nearshore waters. If a significant amount of feeding took place offshore and availability and composition of potential prey was different there, the results of this study would not be totally representative. In addition, the probability of detecting and identifying various

[5]U.S. Department of Commerce, NOAA, Nautical Charts No. 8556 and 16700.

[6]North Pacific Fishery Management Council. 1978. Fishery management plan for the Gulf of Alaska groundfish fishery during 1978. Unpubl. manuscr., 220 p. North Pacific Fishery Management Council, P.O. Box 3136 DT, Anchorage, AK 99510.

prey in the stomachs was not equal. Cephalopod beaks are not always passed through the intestinal tract and may remain in the stomach for several days before they are regurgitated (Pitcher unpubl. data). This increases the probability of detection thereby exaggerating estimates of their utilization.

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PRODUCTION AND GROWTH OF SUBYEARLING COHO SALMON, *ONCORHYNCHUS KISUTCH*, CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, AND STEELHEAD, SALMO GAIRDNERI, IN ORWELL BROOK, TRIBUTARY OF SALMON RIVER, NEW YORK

Decline of lake trout, *Salvelinus namaycush*, and burbot, *Lota lota*, populations in the Great Lakes from 1930 to 1950 created a void of a large offshore piscivore in these waters. Smith (1968) attributed the decline to overexploitation by the commerical fishery and predation by the sea lamprey, *Petromyzon marinus*. The decline was followed by proliferation of the alewife, *Alosa pseudoharengus*, in Lakes Ontario, Huron, and Michigan

(Berst and Spangler 1973; Christie 1973; Wells and McLain 1973). As a result the State of Michigan in 1966 undertook a program to establish coho salmon, *Oncorhynchus kisutch*, in Lakes Michigan and Superior in hopes of creating a valuable sport fishery based on alewife as the major forage species (Tody and Tanner[1]). The success of the Michigan program provided an incentive to other states and provinces bordering the Great Lakes to undertake similar programs.

New York State began its salmonid program for Lake Ontario in 1968 when 41,000 coho salmon were planted in the Salmon River. The following year 70,000 chinook salmon, *O. tshawytscha*, were planted in the Little Salmon River (Parsons 1973). Stocking of steelhead, *Salmo gairdneri*, commenced in 1974 (Parker[2]). Stockings of coho salmon and steelhead have continued annually since their inception. Chinook salmon plantings were stopped after releases in the spring of 1976 because contaminant levels in their flesh generally exceeded action levels for Mirex[3] and PCB's when these fish first became available to anglers as precocious jacks on their maiden spawning run at 1.8-2.7 kg (New York State Department of Environmental Conservation[4]). However, chinook salmon stocking was resumed in 1979.

From its inception, Michigan's salmonid program has given high priority to natural reproduction as a supplement to hatchery production (Tody and Tanner footnote 1). Subsequent studies have focused on the extent of natural reproduction in Michigan (Stauffer[5]) and other ecological aspects of spawning activity (Taube[6]). Reproductive success of Pacific salmonids has been examined in Minnesota (Hassinger et al. 1974) and Wisconsin (Avery[7]). Canadian studies on Great Lakes tributaries have mainly focused on steelhead reproduction (Alexander and MacCrimmon 1974).

In New York, chinook salmon begin their spawning run from Lake Ontario in late August and early September (Jolliff[8]). Chinook salmon redds are present as early as mid-September in the Salmon River in Oswego County. Although most chinook salmon spawning occurs in the Salmon River, smaller tributaries are also utilized. Spawning in smaller tributaries usually does not begin until late September with the peak occurring in mid-October. The selection of larger tributaries such as the Salmon River for spawning is characteristic of chinook salmon in their native range (Stein et al. 1972; Scott and Crossman 1973). Coho salmon run somewhat later than chinook salmon, usually beginning in late September and peaking in late October to early November. Limited coho salmon spawning activity occurs in the Salmon River, possibly because of the large size of the substrate materials. Adult steelhead are present in the Salmon River throughout the fall and into early summer. Steelhead can be found in the smaller tributaries from March through June with most spawning activity occurring in April and May. Stream residence time for juvenile salmonids in the Salmon River system is <1 yr for chinook salmon, up to 1 yr for coho salmon, and up to 2 yr for steelhead (Johnson 1978).

Prior to 1977 the reproductive success of Pacific salmonids was unknown in New York tributaries of Lake Ontario. In 1977, five streams in the Salmon River system were examined for evidence of successful spawning of coho salmon, chinook salmon, and steelhead (Johnson 1978). Initial evidence indicated substantial reproduction of coho salmon and steelhead in some of the streams. The purpose of this study was to quantify reproductive success of Pacific salmonids in one tributary of the Salmon River.

Methods

Orwell Brook was selected as it contained high densities of coho and chinook salmon and steelhead juveniles. Orwell Brook flows for ap-

[1]Tody, W. H., and H. A. Tanner. 1966. Coho salmon for the Great Lakes. Mich. Cons. Dep. Fish. Manage. Rep. 1, 38 p. Fish Division, Michigan Department of Natural Resources, Mason Building, Lansing, MI 48926.

[2]C. E. Parker, Chief, Bureau of Fisheries, New York State Department of Environmental Conservation, 50 Wolf Road, Albany, NY 12233, pers. commun. October 1979.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4]New York State Department of Environmental Conservation. 1977. Monthly report on toxic substances impacting on fish and wildlife. Rep. 1, April 20, 1977.

[5]Stauffer, T. M. 1977. Numbers of juvenile salmonids produced in five Lake Superior tributaries and the effect of juvenile coho salmon on their numbers and growth, 1967-1974. Mich. Dep. Nat. Resour., Fish. Res. Rep. 1846, 29 p. Institute for Fisheries Research, Museums Annex Building, Ann Arbor, MI 48109.

[6]Taube, C. M. 1975. Abundance, growth, biomass, and interrelationship of trout and coho salmon in the Platte River. Mich. Dep. Nat. Resour., Fish. Res. Rep. 1830, 82 p. Institute for Fisheries Research, Museums Annex Building, Ann Arbor, MI 48109.

[7]Avery, E. L. 1974. Reproduction and recruitment of anadromous salmonids in Wisconsin tributaries of Lake Michigan. Dingell-Johnson final Rep., Proj. F-33-R, Study 108, Wis. Dep. Nat. Resour., 32 p.

[8]T. Jolliff, Associate Aquatic Biologist, Bureau of Fisheries, New York State Department of Environmental Conservation, Cape Vincent, NY 13618, pers. commun.

proximately 14.5 km before entering the Salmon River, 17 km from Lake Ontario (Figure 1). About 60% of Orwell Brook is considered adequate for successful salmonid reproduction with suitable substrate generally consisting of gravel (1-2 cm in diameter) and pebbles (3-6 cm in diameter). The maximum summer water temperature recorded during 1977 and 1978 was 21° C. Mean monthly stream discharge from June to October 1978 was 0.26 m^3/s. Salmonids, cyprinids, and catostomids, in order of abundance are the principal components of the Orwell Brook fish fauna.

A single 100 m station was established on Orwell Brook 3 km above the Salmon River. This section was generally characteristic of the lower portion of Orwell Brook. Sections of the stream were visually examined weekly from early May to mid-June in 1978 in order to estimate the approximate time of peak emergence of salmon fry. Peak emergence, as used in this study, occurred when the densities of coho and chinook salmon and steelhead were highest in Orwell Brook. Collections of juvenile salmonids were made monthly from May to October with a 3 m minnow seine. Supplemental observations on salmon emergence were also made in May 1979. Monthly population estimates derived using the Chapman mark-recapture index (Ricker 1975) and average monthly weights of juvenile salmonids were plotted with the area beneath the curve providing an estimate of total production (Chapman 1968). A logarithmic plot assuming an exponential decline in monthly densities was used to determine the population size at peak emergence for coho and chinook salmon. This method, based on the assumption that natural mortality is greatest just after emergence and then gradually diminishes, has previously been employed to estimate the

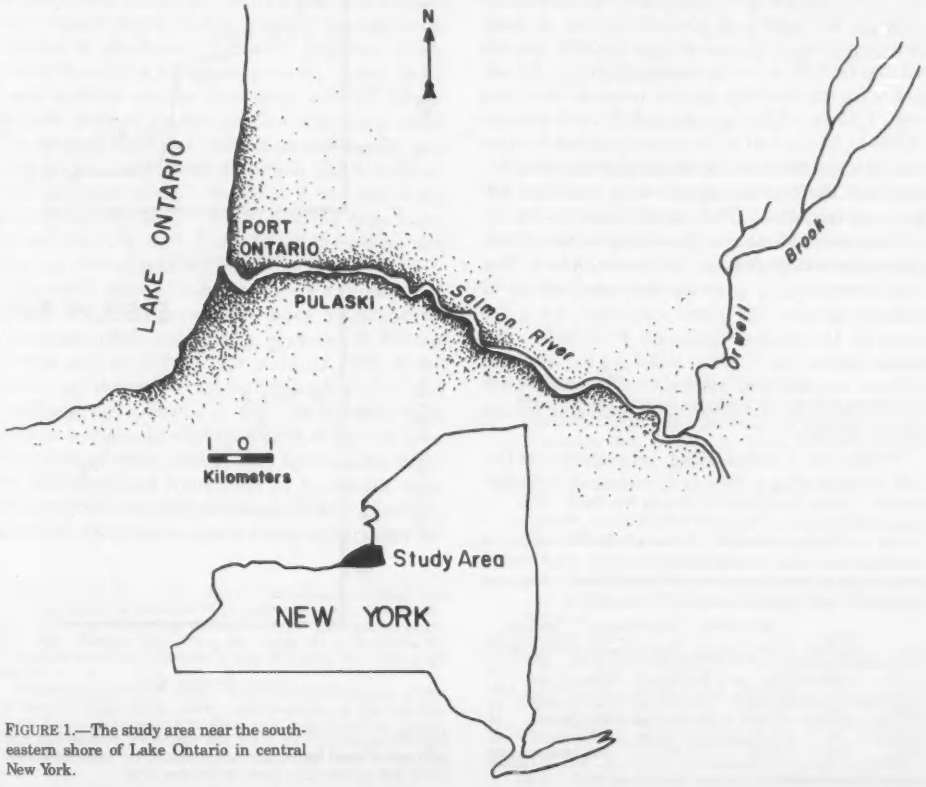

FIGURE 1.—The study area near the southeastern shore of Lake Ontario in central New York.

population size at peak emergence in salmonid populations (Hunt 1966; O'Connor and Power 1976). Total production of each species was divided by the smallest stream area within the 100 m section that was recorded during the study in order to give an estimate of production per unit area.

Results and Discussion

Recently emerged coho and chinook salmon were first observed in Orwell Brook in 1978 on May 13. In 1979, coho salmon were first observed on May 9th and chinook salmon on May 10. Peak emergence of both species occurred during early June 1978. Steelhead began emerging during mid-June and peaked in early to mid-July.

Population estimates were initiated in mid-June about 2 wk after peak salmon emergence. At this time both salmon species were abundant in the main stream and steelhead had started to emerge. Estimates of population size at peak emergence were 718 coho salmon and 189 chinook salmon fry/100 m in the section (Table 1). Densities of fry (number per square meter) at this time were 1.30 and 0.34 for coho and chinook salmon (Table 1). The initial estimate of steelhead in June was 103 fry/100 m or 0.20 fry/m² of stream bottom. However, the highest densities of steelhead fry were not recorded until August (Table 1).

Total production of subyearling coho salmon from 1 June to 30 October 1978 was 1,248 g. This was substantially greater than production of chinook salmon, 282 g and steelhead, 404 g (17 June-10 October) (Figure 2). Production per square meter was 2.7, 0.6, and 0.9 g for coho and chinook salmon and steelhead. Combined total production of the three species was 4.2 g/m² for the period of study.

Production of subyearling coho salmon in Orwell Brook during 1978 was intermediate between

TABLE 1.—Estimated monthly numbers (with 95% confidence limits) and densities (number per square meter) of subyearling coho salmon, chinook salmon, and steelhead in 100 m study area of Orwell Brook, Oswego County, N.Y., during 1978.

Date	Stream area (m²)	Coho salmon		Chinook salmon		Steelhead	
		Number	Density	Number	Density	Number	Density
1 June	553	[1]718	1.30	[1]189	0.34	—	—
17 June	521	500±101	1.04	139±43	.27	103±41	0.20
16 July	483	428±184	.89	121±50	.25	212±72	.44
12 Aug.	489	118±64	.25	51±29	.11	262±84	.56
10 Sept.	476	104±62	.22	36±25	.08	199±58	.42
10 Oct.	495	68±23	.14	31±16	.06	138±34	.28

[1]Logarithmic extrapolation.

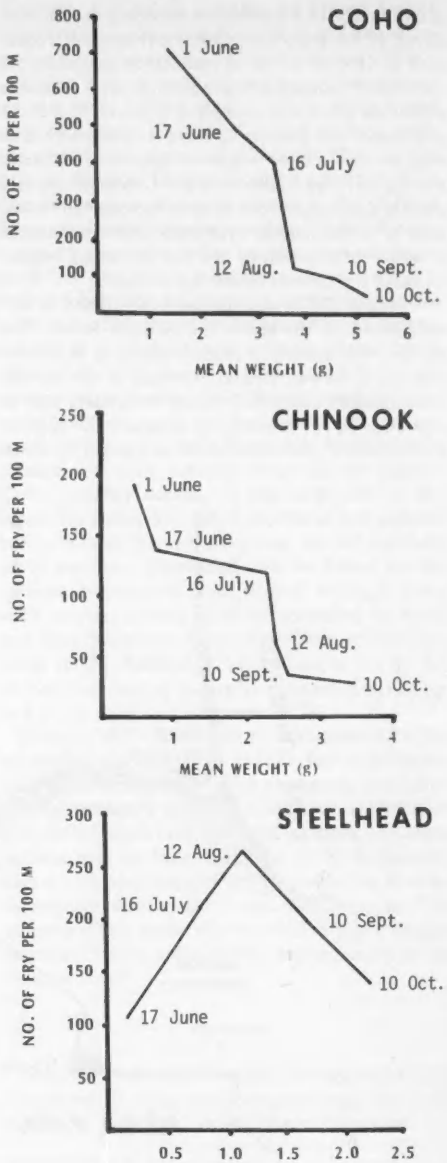

FIGURE 2.—Production curves of subyearling coho and chinook salmon in Orwell Brook, Oswego County, N.Y., 1 June-10 October 1978, and steelhead 17 June-10 October 1978.

that observed in Oregon, 5.6 g/m² (Chapman 1965) and Michigan, 0-1.9 g/m² (Stauffer[9]) during a similar time interval. Production of coho salmon in the 100 m section of Orwell Brook from 1 June to 15 October 1977 was 5.9 g/m² (Johnson 1978). Although the 1978 production estimate for coho salmon represents a 54% decrease from 1977, the variation in production between years is within the range reported by Chapman (1965) for coho salmon in Oregon coastal streams.

No information on chinook salmon production is available for the Great Lakes region; however, production of chinook salmon in Orwell Brook was intermediate to that recorded in the Lemhi River and Big Springs Creek, Idaho (Goodnight and Bjornn 1971). Production of steelhead is less than recorded in Michigan (Hannuksela[10]) and intermediate between the two Idaho streams (Goodnight and Bjornn 1971).

From emergence in May until the termination of sampling in November, subyearling coho salmon were larger than either subyearling chinook salmon or steelhead (Table 2). However, since chinook salmon characteristically leave their natal streams earlier than coho salmon, larger chinook salmon smolts may be migrating early. The growth rate (total length in millimeters per day) of coho and chinook salmon and steelhead was greatest during the first 2 mo following emergence (Table 2). Growth during this 2 mo period was 0.44, 0.47, and 0.39 mm/d for coho and chinook salmon and steelhead (Table 2). High initial growth rates of subyearling coho salmon and steelhead have previously been reported by Chapman (1965) and Stauffer (footnote 9). For the entire period (175 d for salmon, 145 d for steelhead) the growth rates of chinook salmon and steelhead were identical, 0.27 mm/d, with coho salmon being only slightly slower, 0.26 mm/d. In Michigan, growth rates of subyearling coho salmon and steelhead from June to November were 0.29 and 0.26 mm/d (Stauffer footnote 9). However, although these estimates are similar to those obtained in Orwell Brook, both coho salmon and steelhead are initially larger in June in Orwell Brook and this size differential (especially for coho salmon) is retained throughout the fall. There is no available information on chinook salmon growth in the Great Lakes region; however, growth in New York is slower than reported in Washington (Becker 1973).

TABLE 2.—Number examined, mean total length (millimeters) (with 95% confidence limits), and daily growth increments (mm/d) of subyearling coho salmon, chinook salmon, and steelhead from Orwell Brook, May-November 1978.

	Coho salmon			Chinook salmon			Steelhead		
Date	No.	$\overline{TL}$	mm/d	No.	$\overline{TL}$	mm/d	No.	$\overline{TL}$	mm/d
18 May	10	45.1±4.4		10	36.7±3.9				
			0.65			0.34			
17 June	20	63.6±5.7		20	46.7±1.9		10	29.7±1.8	
			0.26			0.61			0.52
16 July	40	71.1±2.8		40	64.5±2.0		30	44.9±1.6	
			0.13			0.06			0.24
12 Aug.	30	74.7±2.5		20	66.0±3.0		25	51.5±1.7	
			0.27			0.11			0.19
10 Sept.	20	82.4±4.9		20	69.2±3.0		30	57.0±3.2	
			0.05			0.22			0.16
10 Oct.	20	83.9±4.9		10	75.7±3.4		25	61.7±3.8	
			0.22			0.28			0.26
9 Nov.	10	90.4±5.2		10	84.0±4.3		10	69.5±4.1	

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ERRATA

Fishery Bulletin, Vol. 77, No. 4

Caillouet, Charles W., Frank J. Patella, and William B. Jackson, "Trends toward decreasing size of brown shrimp, *Penaeus aztecus*, and white shrimp, *Penaeus setiferus*, in reported annual catches from Texas and Louisiana," p. 985-989.

1) Page 987, left colum, last line, correct line to read:
   $\ln F_i = \ln(a) + bC_i + \epsilon$
2) Page 989, Table 3, first line, under Brown shrimp, Texas coast, 1961-1976, correct line to read:
   0.00141* (adding asterisk)

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